THE UNIVERSITY OF MIAMI

THE LARVAL DEVELOPMENT OF SOME WESTERN ATLANTIC LOBSTERS OF THE FAMILY SCYLLARIDAE

BY

Philip B. Robertson

A DISSERTATION

Submitted to the Faculty
of the University of Miami
in partial fulfillment of the requirements for
the degree of Doctor of Philosophy

Coral Gables, Florida

June 1968

THE UNIVERSITY OF MIAMI

A dissertation submitted in partial fulfillment of
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Doctor of Philosophy

Subject

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ACKNOWLEDGMENTS

I am indebted to a number of individuals for providing information and material used in this study. Dr. A. E. F. Heydorn, Prof. Keith Sheard and Dr. D. I. Williamson kindly replied to my inquiries at the beginning of the investigation. Ovigerous females of *Scyllarides aequinoctialis* were obtained through the interest and cooperation of Dr. Phil Dobert, Mr. Jack Hill and Mr. Ray Maloney. Mr. Fred Bedell and Mr. A. J. Mills collected ovigerous females of *Scyllarus americanus*. A phyllosoma collected by R/V CHAIN was called to my attention and shipped by Dr. George D. Grice (Woods Hole Oceanographic Institution). The loan of specimens collected by R/V UNDAUNTED was arranged through Mr. Alexander Dragovich and Mr. Conrad Mahnken (Tropical Atlantic Biological Laboratory, U. S. Fish and Wildlife Service). Specimens deposited at the Florida State Board of Conservation Marine Laboratory were loaned by Mr. Edwin A. Joyce, Jr. and Mr. William G. Lyons. Mr. Lyons generously provided newly hatched larvae of *Scyllarus chacei*, an ovigerous female of *Scyllarus nearctus*, and information concerning *Scyllarides nodifer*. Discussions with Dr. L. B. Holthuis (Rijksmuseum

van Natuurlijke Historie, Leiden) provided much helpful information. Mr. Lester Zukeran (University of Hawaii Marine Laboratory) gave information on the occurrence of _Arctides_. A collection of phyllosomas taken in plankton on the Torgugas Shelf was placed at my disposal by Mrs. Dolores E. Dimitriou (Institute of Marine Sciences). These larvae were obtained by the Institute of Marine Sciences in connection with a study of the distribution of shrimp larvae, supported by the U. S. Bureau of Commercial Fisheries. Subsequent work on the phyllosomas by Robinson and Dimitriou (1963a, b) was supported by the Florida State Board of Conservation. Some specimens from the Gulf of Mexico were from collections by the U. S. Fish and Wildlife research vessel OREGON. Drs. P. M. David and Charles W. Pettitt (National Institute of Oceanography, Wormley, Godalming, Surrey, England) kindly granted permission to examine phyllosomas of the DISCOVERY collection. Dr. Raymond B. Manning (Chairman, Department of Invertebrate Zoology, Smithsonian Institution) loaned the phyllosoma collection of the United States National Museum and the holotype of _Arctus depressus_. Additional specimens were from collections by Mr. Warren Burgess, Mr. David M. Dean, Dr. Hilary B. Moore and Dr. Donald P. de Sylva (Institute of Marine Sciences).

Several persons at this Institute cooperated in bringing

back living material collected on cruises of R/V GERDA, R/V JOHN ELLIOTT PILLSBURY, and other vessels. Operation of the PILLSBURY was financed by a grant for biological ship time from the National Science Foundation. Material was collected by the PILLSBURY with the cooperation of the National Geographic Society-University of Miami Deep-Sea Biology Program.

This study was initiated with the support of a Cooperation Graduate Fellowship from the National Science Foundation. Throughout the investigation I have been associated with the program of larval development of decapod crustaceans, supported by the National Institutes of Health (Grant GM-11244) and the National Science Foundation (Grant GB-4888) through grants to Dr. Anthony J. Provenzano, Jr.

I am grateful to Mrs. C. Edith Marks for assistance in the laboratory throughout this study. Miss Barbara Stolen illustrated the postlarva of *Scyllarus americanus* in dorsal view and assisted in the preparation of graphs for that species. Mr. Robert H. Gore assisted in sorting some plankton samples. Additional help came in various ways from my other associates in the department, Mr. Jorge A. Cabrera, Dr. Sheldon Dobkin, Messrs. Robert A. Feigenbaum, Koesoebiono, Oswaldo Moran-Ribeaux, Talbot E. Murray, John Shoup and Dr. Won Tack Yang.

I especially thank Dr. Anthony J. Provenzano, Jr., committee chairman, for his guidance and encouragement during the study. I am grateful to members of my dissertation committee, Drs. Frederick M. Bayer, Leonard J. Greenfield, Edwin S. Iversen and Donald R. Moore for their helpful suggestions and comments. Dr. Holthuis, Dr. Manning and Mr. Robert A. Smith (Managing Editor, Bulletin of Marine Science) read portions of the manuscript and suggested improvements.

Mrs. Ellen McCormick of the library staff of this Institute has been most helpful in obtaining publications through inter-library loans. Dr. Won Tack Yang translated portions of papers in Japanese. Mr. Donald Heuer (Duplicating Supervisor) reproduced the plates and text.

Finally I must express my gratitude to my wife, Linda, and daughters Beth and Kathy, for their understanding of the demands on my time required by this study.

Philip B. Robertson

Miami, Florida
June, 1968

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PART I

INTRODUCTION

The Scyllaridea comprise two families of marine decapod crustaceans, the Palinuridae, known as spiny or rock lobsters, and the Scyllaridae, known by a variety of common names such as shovel lobster, slipper lobster and sand lobster. Both groups are widely distributed in tropical to temperate seas. Several genera and species of palinurids support commercial fisheries in various regions. Many scyllarid lobsters are said to be of excellent eating quality, but most apparently are not found in sufficient abundance to be of much economic importance. Certain species are exploited locally; others may have undeveloped fishery potential (see Butler and Pease, 1965; Chace, 1966).

Both families possess a characteristic pelagic larval form known as the phyllosoma. These larvae are remarkable for the dorsoventrally flattened, leaf-like body, their transparency, and the large size (up to 80 mm) which some attain. Phyllosomas hatch at a length ranging from about 1 to slightly over 3 mm, depending on the species, and pass through a number of planktonic stages, drifting more or less passively with prevailing water currents. The last phyllosoma stage, through a metamorphosis which Gurney (1942) has

termed "The most profound transformation at a single moult known among Decapoda," produces a postlarval form structurally similar to the adult.

Although the larval development of scyllaridean lobsters has received the attention of a number of investigators, our knowledge of the life histories of these crustaceans has remained limited. This can be attributed to difficulties in: (1) obtaining a complete developmental sequence, owing to the long series of stages between hatching and metamorphosis, coupled with their offshore or oceanic distribution and the very low frequency of appearance in plankton hauls of the various stages of many species; (2) identifying phyllosomas with the parent species, and in identifying early larvae, including those of known identity hatched in the laboratory, with later stages taken in plankton, because of the relatively great increases in size and changes in morphology which occur during development; and (3) maintaining phyllosoma larvae in the laboratory for any length of time.

The systematics of the various forms of phyllosoma larvae is unsatisfactory, the adult species to which they belong being known in relatively few cases. In most instances little or nothing is known concerning their biology. On several occasions phyllosoma larvae have been assigned, with no other evidence, to the most common adult known from a particular geographic region. Since planktonic larvae can seldom be identified with certainty, particularly in

areas where the fauna is poorly known or where numerous genera and species are present, questionable identifications have been introduced into the literature. These have often been accepted and perpetuated by subsequent investigators. The rather large international literature dealing with phyllosoma larvae consequently needs critical review and integration.

A comparison of the various forms of phyllosoma larvae should contribute to an understanding of the natural affinities within the Scyllaridea. For instance, Gurney (1936) attributed to the Scyllaridae forms tentatively described as "*Thenus*" and "*Parribacus*," while stating:

> . . . such an identification I am most reluctant to accept, for the reason that both these forms seem much more closely to resemble the Palinuridae, and if they are really Scyllaridae, there are two quite distinct types of scyllarid Phyllosoma. This would imply a separation of the Scyllaridae into two groups, a separation which cannot, so far as I know, be justified on adult structure.

Data concerning the growth of phyllosoma larvae, the number of larval stages and duration of larval life are essential to an understanding of the biology of the adult. The distribution of the latter must depend in part on the duration of larval life and the nature of the currents to which the larvae are exposed. Accurate information is lacking for most species of scyllaridean lobsters. Much of our present knowledge has been derived indirectly through studies of planktonic material.

With the hope that it might be possible to fill some of the gaps in our knowledge of this interesting and important group of crustaceans, I undertook investigations early in 1964 at the suggestion of Dr. Anthony J. Provenzano, Jr. Studies were carried out on representatives of both families. At that time there was a virtually complete lack of information concerning the larval development of western Atlantic species, with the exception of the spiny lobster of commerce, *Panulirus argus* (Latr.) (Lewis, 1951; Ingle *et al*., 1963).

Since the present studies were initiated, results have been published of investigations by Sims and associates at the Florida State Board of Conservation Marine Laboratory (Sims, 1964, 1965a, b, 1966a, b, 1968; Sims and Ingle, 1967) and by Baisre (1964, 1966) in Cuba. Despite these investigations, the larvae of no species of western Atlantic scyllaridean lobster can yet be identified with certainty. With the exception of unsuccessful experiments by Crawford (1920) and later by Sims (unpublished), I am aware of no attempts to rear in the laboratory the larvae of any western Atlantic species.

The scyllarid lobsters are grouped in the following seven genera: *Evibacus*, *Ibacus*, *Thenus*, *Scyllarus*, *Scyllarides*, *Parribacus* and *Arctides*. The last four are represented in the western Atlantic -- *Scyllarus* and *Scyllarides* each by five species, and *Parribacus* and *Arctides* each by a single species. A second species of *Parribacus*, *P. parrae*

(H. Milne-Edwards), has been described from the West Indies, but Holthuis (1946) considered it probable that "*P. parrae* is identical with *P. antarcticus* and is only founded on an aberrant or damaged specimen." Table 1 lists the known species of western Atlantic Scyllaridae, including a recently discovered species of *Scyllarus* to be described by Dr. L. B. Holthuis.

The results of my investigations on the larval development of the Scyllaridae are presented in this work. I have attempted to recognize and define the generic and specific characters of the various forms of scyllarid phyllosoma larvae found in the western Atlantic, and to identify these larvae with the parent species. Representative stages are described and illustrated. A provisional diagnosis is provided for each form. The postlarval stage of three species of *Scyllarus* is also described. A provisional key to the scyllarid phyllosomas of the western Atlantic is included, and a key for the generic determination of phyllosomas of both families on a world-wide basis. The possible significance of larval characters in revealing natural affinities within the Scyllaridea is discussed.

Data on the molting, growth, number of stages and duration of larval life are given for larvae of four species of *Scyllarus* and one species of *Scyllarides* reared in the laboratory. I am happy to report the first successful attempt to rear the larvae of any species of scyllaridean lobster through all phases of development from hatching to the

postlarval stage. There are no previous reports on the larval development of any species of *Scyllarides* in the laboratory. I could not obtain ovigerous females of *Parribacus* or *Arctides*, the adults of which are relatively uncommon in the western Atlantic. Distributional data are presented for phyllosomas collected in the plankton.

The literature dealing with the larval development of scyllarid lobsters is critically reviewed and integrated in the light of present findings.

TABLE 1

LIST OF THE SPECIES OF WESTERN ATLANTIC SCYLLARIDAE

Genus *Arctides* Holthuis	*Arctides guineensis* (Spengler, 1799)
Genus *Parribacus* Dana	*Parribacus antarctious* (Lund, 1793)
Genus *Scyllarides* Gill	*Scyllarides aequinoctialis* (Lund, 1793)
	Scyllarides brasiliensis Rathbun, 1906
	Scyllarides deceptor Holthuis, 1963
	Scyllarides delfosi Holthuis, 1960
	Scyllarides nodifer (Stimpson, 1866)
Genus *Scyllarus* Fabricius	*Scyllarus americanus* (Smith, 1869)
	Scyllarus chacei Holthuis, 1960
	" *faxoni* Bouvier, 1925
	" *nearctus* Holthuis, 1960
	Scyllarus n. sp.

PART II

HISTORICAL REVIEW

One of the first records of a phyllosoma larva is by Forster (1781), who described under the name *Cancer cassideus* what is unmistakably a phyllosoma belonging to the Scyllaridae. In 1817 Leach established the genus *Phyllosoma*, and in following years the larval forms of the Scyllaridea, sometimes known as "glass crabs," were described as adults under this generic name. The results of early investigations were included in a monograph by Guerin (1833). Milne-Edwards (1837) gave a comprehensive account of the genus, which he placed in the Stomatopoda, and according to the configuration of the abdomen, divided it into three groups, the *Phyllosomes ordinaires*, *Phyllosomes brevicaudes* and *Phyllosomes laticaudes*.

Two decades later evidence began to indicate that the forms known as Phyllosoma might be larval stages of the Scyllaridea, but there was an unfortunate period of confusion and controversy, which has been reviewed by Richters (1873), Cunningham (1891) and von Bonde (1930). Sims and Ingle (1967) recently stated that "It was not until the early 1900's that many zoologists simultaneously discovered that the phyllosoma were the larval stages of spiny lobsters."

The issue was actually resolved more or less beyond doubt in 1870, when Dohrn described the development of Scyllarus in the egg and the newly hatched phyllosoma.

The attention of investigators was then directed toward establishing the generic and specific identities of the various forms of phyllosomas and to reconstructing the life histories of various species of Scyllaridea. Richters (1873) published an important paper, based on a study of a large collection from the Hamburg Museum, which showed that the Phyllosomes ordinaires of Milne-Edwards were larvae of the Palinuridae and that the Phyllosomes brevicaudes and laticaudes belonged to various genera of Scyllaridae.

A number of subsequent papers appeared describing phyllosomas, many of uncertain parentage, collected in the plankton, and the first stage of a few species was described from larvae hatched in the laboratory. The most comprehensive attempt to classify phyllosoma larvae was by Gurney (1936), who concluded that "it cannot be claimed that any real progress is made in identifying these forms, and even the question of the recognition of generic or specific characters is left uncertain." He wrote, "It is difficult to see how further progress can be made in systematic knowledge of Phyllosoma. . . ."

Our knowledge of phyllosoma larvae has advanced in recent years, but is still far from satisfactory. Among the Scyllaridae, the phyllosomas of Ibacus are relatively well known (Richters, 1873; Haswell, 1879; Balss, 1914; Tokioka,

1954; Harada, 1958; Saisho and Nakahara, 1960; Tokioka and Harada, 1963; Dotsu, Seno and Inoue, 1966; Dotsu *et al*., 1966). The larval characters of *Thenus*, after considerable confusion, have been established by Prasad and Tampi (1957). Gurney (1942) believed that the larvae characteristic of *Scyllarus* and *Scyllarides* "are known with certainty or probability," but this is open to question. Saisho (1962b, 1966b) described the first three stages of *Parribacus* from laboratory reared material, and Sims (1965a, 1968) attributed to this genus later stages from the plankton. At the time of writing, Dr. M. W. Johnson is said to have a paper in press (Crustaceana) describing larvae of *Evibacus*, a monotypic genus apparently restricted to the Pacific coast of the Americas. The phyllosomas of *Arctides* are unknown.

The desirability of observing the development of phyllosoma larvae in the laboratory has long been recognized, but as Allen (1916) stated, "Their extreme delicacy and pelagic habit make their culture an especially difficult problem." Early attempts to rear larvae of various species of Scyllaridea proved unsuccessful. W. von Bonde (1930) felt that "such efforts are almost always doomed to failure, because it would be well-nigh impossible to offer the larvae in their various stages of development environs and conditions similar to those for which nature has specially adapted them." However, C. von Bonde (1936: 18) reported that by using a specially designed hatching box, he had been able to obtain phyllosomas of *Jasus lalandii* (H. Milne-Edwards) "of various

sizes between 3.8 mm and 24 mm and they are to be described in a paper entitled 'Experiments in artificial hatching and rearing of the Cape Crawfish *Jasus lalandii*.' Inv. Rept. No. 9, Fish and Mar. Biol. Survey, S. Afr. (in preparation)." This paper unfortunately was never published. In 1964 I inquired of the Division of Sea Fisheries, Cape Town, South Africa, but was unable to obtain a manuscript. Sheard (1949) reared larvae of *J. lalandii* through five molts using containers in wells of boats in open waters.

With the development of improved culture techniques and the availability of nauplii of the brine shrimp *Artemia salina* (L.) as a source of food, limited successes have been achieved in recent years in attempts to rear in the laboratory the larvae of a few species of both palinurid and scyllarid lobsters (Nonaka, Ohshima and Hirano, 1958; Saisho and Nakahara, 1960; Saisho, 1962a, b; Inoue and Nonaka, 1963; Inoue, 1965; Johnson and Knight, 1966; Saisho, 1966b; Ong, 1967). Dotsu, Seno and Inoue (1966) have reared early phyllosomas of two species of *Ibacus* using larval gobiid fishes as food. Although phyllosomas have been maintained through several early stages, in no instance until now has it been possible to study the complete larval history of any species by rearing larvae through all phases of development to the postlarval stage.

The only report dealing with the larval development of *Scyllarus* in the laboratory is by Saisho (1966b). He (1964b) reported an unsuccessful attempt to rear phyllosomas of *S.*

bicuspidatus (de Man) with brine shrimp as food, but later was able to rear larvae of this species through eight molts. Prasad and Tampi (1960) mentioned that attempts were being made to rear larvae of *S. sordidus* (Stimpson).

Our knowledge of the larval development of western Atlantic scyllarid lobsters until recently consisted of only a few isolated descriptions. A scyllarid phyllosoma collected in the West Indies by the CHALLENGER was mistakenly referred to *Panulirus* by Bate (1888). Ortmann (1893) reported a large scyllarid phyllosoma from the South Equatorial Current off Brazil near Fernando Noronha. Verrill (1922) discussed the form of phyllosoma described by Bate and suggested that it "may belong to *Scyllarus* or one of the species of *Scyllarides*, but its origin is very uncertain." A first stage phyllosoma from Bermuda was referred to *Scyllarides* by Gurney (1936), and Lebour (1950) also attributed to *Scyllarides* two different stage I phyllosomas from the plankton around Bermuda. Gurney (1936) listed three phyllosomas of *Scyllarus* taken by the DISCOVERY off the coast of Brazil and illustrated parts of one specimen.

Robinson and Dimitriou (1963a, b) presented data on the occurrence of phyllosoma larvae in waters of the Tortugas Shelf. They found that most of them appeared to belong to the genera *Scyllarus* and *Scyllarides*. Ingle *et al*. (1963) mentioned that larvae of *Scyllarus* were taken off the western coast of Florida. Sims (1964) described four

large scyllarid phyllosomas of uncertain identity collected in the Yucatan and Florida straits. A phyllosoma in a late stage of development was illustrated by Baisre (1964), who assigned it to *Scyllarus* sp. Sims (1965a) attributed to *Parribacus* a sequence of phyllosoma stages from the plankton, and gave data on their distribution. The stage I phyllosoma of *Scyllarus americanus* was described by Sims (1966b) from specimens hatched in the laboratory. He stated that numerous phyllosomas of *Scyllarus* had been collected in the Gulf of Mexico. Baisre (1966) described from planktonic material a sequence of six phyllosoma stages belonging to *Scyllarus* sp., and gave data on the distribution of these stages in Cuban waters. Sims (1968) has recently reported from the North Atlantic phyllosomas attributed to *Scyllarus*, *Scyllarides* and *Parribacus*. The bibliography compiled by Sims (1966c) is a useful guide to the literature dealing with both families of Scyllaridea.

PART III

MATERIALS AND METHODS

The larval development of scyllaridean lobsters may be investigated by any or all of the methods summarized by Ewald (1965) for study of the early life history of penaeid shrimp. These involve: (1) description of individual larvae from the plankton which show similarities to previously described forms; (2) construction of a developmental sequence, by linking together two or more forms from the plankton showing morphological similarities; (3) rearing larvae found in the plankton through one or more stages; (4) rearing larvae hatched from eggs of known parentage through one or more stages. The most satisfactory results are usually obtained through a combination of the various methods. All were utilized in the present study.

Plankton samples collected over a period of several years during various investigations in the western Atlantic by Institute of Marine Sciences research vessels were examined for phyllosoma larvae. Phyllosomas were removed, examined under the microscope, and arranged in sequences according to form, size and morphological development. The collection of phyllosoma larvae dealt with by Robinson and Dimitriou (1963a, b) was examined. These were obtained

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from plankton samples collected in the Tortugas Shelf region in connection with a study of the distribution of shrimp larvae by Jones et al. (1963). The phyllosoma collection of the United States National Museum (USNM) was borrowed, as were some additional specimens collected by the exploratory fishing vessel OREGON, the Florida State Board of Conservation Marine Laboratory, the Tropical Atlantic Biological Laboratory of the U. S. Fish and Wildlife Service, and the Woods Hole Oceanographic Institution. I had the opportunity to examine some of the phyllosomas in the DISCOVERY collection treated by Gurney (1936), parts of which are now deposited at the National Institute of Oceanography, Wormley, Godalming, Surrey, England.

Attempts were made to hold living phyllosomas captured in plankton through at least one ecdysis in the laboratory to confirm sequences of stages and to facilitate identification of unknown larvae by observation of metamorphosis to identifiable postlarval stages. Gurney (1936) noted:

> . . . conclusive specific determination can only be got by capture of the last stage and observation of the moult to the natant stage. As the late phyllosomas are high-sea forms, apparently confined to the deeper layers, and only accessible to well-equipped oceanographical expeditions, such observations cannot be expected.

During the present study late-stage phyllosomas of the Scyllaridae, though never abundant, were taken in plankton nets towed near the surface at night and were occasionally captured at greater depths during the day in the Isaacs-Kidd

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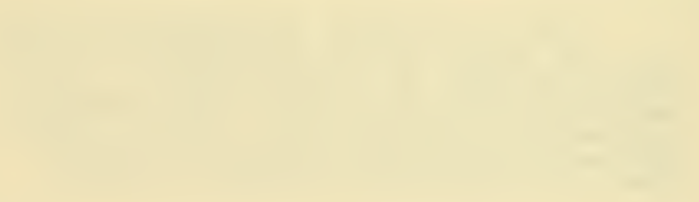

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midwater trawl (IKMT). On several occasions it was possible to remove specimens in good condition. These phyllosomas, depending on their size, were placed in compartments of plastic trays or in ½-gallon jars. They were returned to the laboratory, where the water was changed usually every second day. Attempts were made to feed them *Artemia* nauplii and small pieces of shrimp, but with little apparent success. Upon ecdysis the cast was preserved and later compared with the stage produced.

The third basic area of effort was in hatching eggs from females and study of the larvae in the laboratory. Ovigerous females of *Scyllarus* were sometimes collected in otter trawls by research vessels of this Institute and the Florida State Board of Conservation. The aid of commercial fishermen in the south Florida area was enlisted to obtain egg-bearing females of species which are frequently taken in lobster traps and shrimp trawls. A modest cash reward was offered to a few reliable individuals. Ovigerous females were brought to the laboratory and held usually in glass aquaria provided with running sea water. In a few instances specimens of *Scyllarus* were maintained in bowls or in compartments of a plastic tray.

The rearing technique was essentially the one which has proven successful at this laboratory for rearing larvae of various anomurans, caridean and penaeid shrimps, and brachyuran crabs. Newly hatched larvae were pipetted or dipped from the aquaria and placed individually in numbered

compartments of transparent plastic, 18-compartmented trays. Trays of two different sizes, manufactured by Vlchek Plastics Company, Middlefield, Ohio, were used in the experiments. Each compartment contained 15 to 20 or 50 to 75 ml of sea water passed through Pyrex wool filtering fibre. Additional larvae were usually mass cultured in fingerbowls and larger containers.

Sea water from two different sources was used for rearing larvae -- water from Biscayne Bay adjacent to the laboratory, and water collected several kilometers offshore in the Florida Current and stored in 5-gallon glass carboys or polyethylene containers. Larvae were usually reared at different temperatures. Temperature was controlled by thermal cabinets equipped with recording thermometers. Except for one instance involving starved larvae, the quality and quantity of light were not controlled beyond avoiding exposure of larvae to direct sunlight. In a few instances larvae were reared at reduced salinities.

The phyllosomas were fed recently hatched nauplii of Artemia salina and were transferred to freshly prepared trays daily or every second day. The density of brine shrimp nauplii was not controlled. Trays of starved phyllosomas were usually maintained. The first one or two stages were transferred with a 5.3 mm-bore pipette; later stages were transferred with a dipper made from a small plastic spoon.

Each compartment was checked daily for exuviae and dead

larvae. The condition of each larva was recorded. Starved individuals were considered dead when they began to turn opaque. Exuviae and specimens of each stage were preserved in 5-10 per cent formalin buffered with hexamethylenetetramine or in 70 per cent ethanol.

Drawings of the entire animal and detailed illustrations of pertinent appendages were made for various stages of the different forms. All are original unless otherwise acknowledged. Illustrations of whole larvae were made with the aid of a Bausch & Lomb microprojector, using different lenses and focal lengths to give the desired magnification. Details were checked microscopically at higher magnifications. All phyllosomas are illustrated in ventral view. Since they are bilaterally symmetrical, the images have in some instances been transposed to facilitate drawing or comparison, so that appendages of one side of a larva may appear on the opposite side in the illustration. The numerous setules present on the natatory setae of the exopods have been omitted in all drawings of entire larvae.

Enlarged drawings of appendages were made whenever possible from entire specimens without dissection, with the aid of the microprojector or a camera lucida on a Wild M-5 or M-20 microscope. When necessary for greater clarity, appendages were dissected in water or glycerine, stained with Mallory's acid fuchsin red or lignin pink, and mounted on a slide or glass coverslip. Setules and spinules are represented semidiagrammatically. Notes of chromatophores

were made from living immobilized specimens or from freshly killed individuals in sea water. Chromatophores are indicated by stellate marks in illustrations of stage I phyllosomas.

The postlarva of Scyllarus americanus was cleared in 5 per cent KOH and illustrated with the aid of a camera lucida on a Wild M-5 microscope. The postlarva of Scyllarus nearctus was drawn from an intact specimen.

Measurements of specimens up to total length about 8 mm were made with an ocular micrometer. Total length (TL) was measured ventrally from the anterior tip of the fore-body (cephalic shield) between the eyestalks to the posterior margin of the abdomen (telson when present) in the midline. Phyllosomas from the plankton, unless they can be referred to a certain stage with some probability, are reported by total length rather than by an arbitrarily assigned stage.

The term "stage" is used in the sense of intermolt. Although Saisho (1966a) has proposed that "instar" be used in this sense, I have avoided the latter term because it may have a somewhat different connotation in other groups of arthropods. The values for duration of stages are based on the time between molts for larvae which completed the ecdysis to the next stage. The growth factor, an index of the length increase at an ecdysis, represents the ratio of the total length of a stage to that of the preceding stage. The final phyllosoma stage is the last stage prior to metamorphosis.

A schematic drawing of a phyllosoma larva, indicating

the external morphology, is given in figure 1.

A separate Materials and Methods section and a Discussion are provided in the text dealing with each species.

PART IV

RESULTS

A. Scyllarus americanus (Smith)

Materials and methods. Adults of S. americanus were taken in shrimp trawls by commercial bait shrimpers operating in Barnes Sound, located between the southeastern end of the Florida mainland and the western side of upper Key Largo, and in South Biscayne Bay, Florida. Ovigerous females were obtained in January and March, 1965 and in April, 1966. They were held in the laboratory in 2½- or 5-gallon aquaria provided with running sea water.

Recently deposited eggs were bright yellow and slightly elliptical, measuring 0.43 by 0.47 mm. They required two to three weeks at temperatures between 20° and 25° C to develop to the point of hatching, at which time they were more or less spherical and 0.62 to 0.65 mm in diameter. A female 20.8 mm in carapace length and 59.5 mm in total length carried approximately 8,000-9,000 eggs.

Although in some instances the eggs were torn off by the female prior to hatching or the embryos were liberated from the egg capsules in a non-viable condition, broods of larvae were obtained on three separate occasions. Hatching took place late at night or in the early morning. Water

temperature in the aquaria at times of hatching was 25 ± 1° C; salinity was 36 ± 1°/oo. As reported by Sims (1966b), the newly hatched larvae were in the first phyllosoma stage; no free-swimming prephyllosoma stage was observed.

Larvae were reared at 10°, 15°, 20°, 25° and 30°C in 100 per cent sea water, at 20°, 25° and 30°C at salinities of 32.7, 29.3 and 25.8 °/oo, and at 23.2 °/oo at 25°C only. Larvae to be reared at reduced salinities were placed in a bowl containing a measured volume of bay water at 36.9 °/oo and the salinity was progressively lowered over a period of 15-24 hours by adding a few mls of distilled water at intervals. Groups of larvae were removed from the bowl and placed in individual compartments of trays containing water at the salinity corresponding approximately to that in the bowl at the time of their removal. Trays of starved individuals were placed at 15°, 20°, 25° and 30°C in 100 per cent sea water.

The females are deposited in the Invertebrate Museum of this Institute (Acc. Nos. 32.3366, 32.3367, 32.3368).

The scales on all illustrations of entire larvae represent 1.0 mm. Those on drawings of appendages and other parts represent 0.5 mm except where labeled otherwise.

I examined the collection of phyllosomas from the plankton of the Tortugas Shelf region previously dealt with by Robinson and Dimitriou (1963a, b). Details of sampling are given in their papers and in Jones _et al_. (1963). Robinson and Dimitriou found scyllarid larvae to be far more common

than those of Panulirus. The majority of specimens proved by comparison with reared material to be larvae of S. americanus. Representative reared and planktonic stages are deposited in the Invertebrate Museum of this Institute (Acc. No. 32.3595).

Results. In no instance did starved larvae molt (fig. 2). They lived at 30°C until five days after hatching, and at 25°, 20° and 15°C survived respectively for an average of 6.2, 7.6 and 8.8 days. There was no significant difference in survival at 20° and 25°C between starved individuals exposed to a diurnal cycle of light and dark and those kept in continuous darkness.

Although some individuals from each of three different broods reached the final phyllosoma stage of development in the seventh stage, metamorphosis to the postlarva occurred only among larvae of one group reared in various salinities at 25°C (fig. 3). Postlarvae were produced from metamorphosis of stage VI phyllosomas at 32.7 °/oo, from both stage VI and VII larvae at 29.3 °/oo, and only from stage VII phyllosomas at 25.8 °/oo. Few larvae died during the early stages, but mortality became appreciable toward the end; only about 10-20 per cent survived to the postlarva. Table 2 gives the duration of the larval stages for each individual which reached the postlarval stage. Postlarvae were obtained in a minimum of 32 and a maximum of 40 days after hatching. All died without molting within three days after metamorphosis.

TABLE 2

DURATION IN DAYS OF THE PHYLLOSOMA STAGES OF THE NINE INDIVIDUALS OF *SCYLLARUS AMERICANUS* WHICH REACHED THE POSTLARVAL STAGE IN VARIOUS SALINITIES AT 25° C

Stage	32.7 °/oo			29.3 °/oo				25.8 °/oo	
I	4	4	4	4	5	4	4	5	5
II	4	4	4	4	4	4	4	4	4
III	4	4	4	3	4	4	3	4	5
IV	4	4	5	4	4	4	4	4	4
V	6	6	6	5	6	5	5	4	4
VI	11	12	12	12	12	7	8	8	7
VII	--	--	--	--	--	10	10	11	11
Total Duration	33	34	35	32	35	38	38	40	40

At 20°C a few individuals in each of the above salinity levels reached the seventh stage but failed to undergo metamorphosis (fig. 4). The deleterious effect of reduced salinity in combination with lower temperature was evident at 25.8 °/oo. A number of larvae were unable to free themselves completely from their exuviae at the first ecdysis and eventually died without reaching the next stage. In a different experiment a few larvae reared at 25°C in a salinity of 23.2 °/oo reached the final phyllosoma stage and one individual died in the process of metamorphosis on the forty-sixth day after hatching. The data do not warrant conclusions concerning the effect of salinity on the development of *S. americanus*, but they suggest that the duration of larval life may be somewhat longer at lower salinities.

The effect of temperature on development at salinity which varied from 35.6 to 38.6 °/oo is shown in fig. 5. The duration of the various stages was longer at lower temperatures, with the exception that at 10°C the larvae were nearly immobilized and died without molting after little more than one week. At 15°C only marginal development was possible; the first stage was prolonged to more than three weeks, and none of the individuals which eventually molted to the second stage reached the third. Larvae at 20°C survived to the seventh, eighth and in one instance to a ninth stage but failed to metamorphose. In this experiment larvae at 25°C which reached the final phyllosoma in stage VII died without subsequent ecdysis. Some of the individuals in

stage VII were more or less intermediate between the subfinal and final phyllosoma stages, having failed to attain the full morphological development characteristic of the final stage. A few individuals molted to an eighth phyllosoma stage. At 30°C the duration of each stage was slightly shorter than at 25°C, but mortality was higher and few larvae survived to stage VII.

In most of the experiments the molting frequency was relatively consistent during the first few stages. The duration of the later stages became increasingly variable and the mean duration increased at the fifth or sixth stage as shown in fig. 6. Among those individuals which produced postlarvae from stage VI, the duration of the final phyllosoma stage was about twice that of the subfinal stage and three times that of each preceding stage (see Table 2). The mechanisms which control the regular sequence of molts in larval forms are not fully understood. Costlow (1965) has suggested that early in larval development only the molt-accelerating hormone of the Y-organ is present and that late in development, perhaps at the beginning of the megalops stage in Callinectes sapidus, the X-organ sinus gland complex of the eyestalk becomes functional, producing the molt-inhibiting hormone which prolongs the intermolt period and eliminates the established frequency of molting of the zoeae. If this is the case, the present data suggest that molt-inhibiting hormone may begin to be produced in the subfinal phyllosoma stage of S. americanus, prolonging the duration

of the last two stages and allowing additional time for reorganization of the larva prior to the metamorphic molt. Molting may be inhibited by simultaneous demands made on the organic reserves in preparation for metamorphosis (see Passano, 1960). The observed increase in duration could be due in part to less than optimum conditions in the laboratory, although a similar extension of duration has been found by Provenzano (1968) for the last zoeal and glaucothoe stage of the hermit crab Petrochirus diogenes (L.).

Use of the larger tray for rearing gave no better results than the smaller size and only made it more difficult to provide a concentration of brine shrimp nauplii. In the experiment which produced postlarvae, the phyllosomas were reared in the smaller trays and the water was changed daily until stage II and every second day thereafter.

Phyllosomas from the plankton show general agreement with laboratory reared larvae in the number of stages. It is difficult to assign some individuals to a definite stage because of overlap in the degree of morphological development between stage IV-V and V-VI. This is probably due in part to larvae attaining the final phyllosoma stage, which is well-defined by the presence of gill buds, in either the sixth or seventh stage.

The total length and growth of laboratory reared and planktonic larvae are compared in Table 3, assuming in each case for comparative purposes that the larval life consists of seven phyllosoma stages. The data show that the growth

TABLE 3

GROWTH OF REARED AND PLANKTONIC LARVAE OF *SCYLLARUS AMERICANUS*

	Range TL		Mean TL		Growth factor	
Stage	reared	planktonic	reared	planktonic	reared	planktonic
I	1.5-1.7	1.5-1.7	1.6	1.6		
II	2.2-2.4	2.2-2.4	2.3	2.3	1.44	1.44
III	2.9-3.4	2.9-3.8	3.2	3.5	1.39	1.52
IV	3.9-4.8	3.9-5.9	4.3	5.0	1.34	1.43
V	4.9-6.6	5.3-7.1	5.7	6.5	1.33	1.30
VI	5.6-8.5	7.1-9.8	7.3	8.6	1.28	1.32
VII	8.3-10.2	9.7-13.0	8.9	11.2	1.22	1.30
PL	6.4-7.0	--	6.8	--	0.76	

The figures for each stage, with the exception of the postlarva, are based on measurements of at least 10 individuals. The growth factor represents the ratio of the total length of a stage to that of the preceding stage.

of larvae reared in the laboratory fell behind that of individuals from the natural environment at the second ecdysis and that reared larvae in subsequent stages were somewhat smaller on the average than corresponding stages from the plankton. Many of the planktonic specimens are also somewhat more advanced morphologically beginning at the third stage than most reared larvae believed to be in corresponding stages. If it is assumed that larvae from the plankton attain the final phyllosoma stage in stage VI, the growth factor for the last two stages falls between 1.4 and 1.5.

Diagnosis of the Phyllosoma

Exopod of pereiopod 2 in stages I and II respectively with 8 and 9 pairs of natatory setae; apical article of maxilla 2 with three plumose setae. Fore-body in subsequent stages subcircular in outline. Length of final phyllosoma about 9-13 mm.

Characters of the Phyllosoma

The fore-body in stage I is slightly wider than long and nearly twice the width of the hind-body. By stage III the fore-body has become slightly longer than wide and its outline has assumed the shape of a circle drawn out obtusely anteriorly and posteriorly. In subsequent stages the fore-body retains a subcircular outline and remains about 1.1 times longer than wide. Its width relative to

the hind-body decreases somewhat, being in the final stage 1.5-1.6 times that of the latter.

The abdomen in early stages is narrow and more or less parallel-sided, with a short, obtuse spine and three small setae at each posterolateral angle. In later stages the abdomen becomes broad at the base, forming a tapering continuation of the hind-body. In the final stage it is about 4/5 the length of the hind-body and the segments are marked off dorsally near the midline. The spines at the posterolateral angles remain short and inconspicuous throughout development. In the final stage they are situated well above the level of the posterior margin of the telson.

The eye in stage I is not stalked and is about as long as the antennule. The eye becomes stalked at stage II. In later stages the eye and stalk are 1.3-1.5 times the length of the antennule.

The antennule in stage I has a small seta medially slightly beyond the middle of its length, and is provided with three terminal aesthetascs plus a small spine or seta at the inner distal angle. In stage II the terminal tuft consists of four aethetascs, plus an additional small seta at the outer distal angle. A second tuft of aesthetascs is added proximally. The inner flagellum is differentiated in stage II as a short conical protuberance bearing the small seta at its tip. In subsequent stages the inner flagellum increases in length, becoming in the final stage as long as the outer flagellum. At each ecdysis aesthetascs are added

in tufts of up to four along the distomedial portion of the latter. At stage IV the outer flagellum if clearly marked off from the peduncular portion, which consists of two distinct segments. In the next stage the antennular peduncle has three more or less distinct segments, the lengths of which in the final stage are in the approximate ratio 100:85:63 from proximal to distal.

The antenna in early stages is uniramous and short, with a small seta on each side near the distal end. In specimens from the plankton a protuberance on the outer side of the proximal portion may be indicated in stage III. In stage IV this appears as a small, distinct triangular process, which becomes larger in subsequent stages. The antenna gradually increases in length but is never as long as the antennule. In the final stage the antenna is broad and a division is indicated in the subcuticular tissue distal to the outer process. The medial margin of the distal portion is shallowly crenulate and provided with a few small setae.

Maxilla 1 is biramous, without palp. The coxal endite in stage I bears one stout, elongated terminal seta and one shorter but similar seta, plus one small terminal and one subterminal spine or seta. The basal endite has two strong terminal teeth plus two small subterminal spines or setae and a small seta proximally the anterior margin. The basal endite acquires a third terminal tooth at stage IV. A few spines or setae are added to each endite during development.

Maxilla 2 in early stages consists of an elongated

basal segment and a small, narrow apical article which bears three long, plumose setae. I found no variation in the number of setae among several specimens examined from different broods. At the ecdysis to stage IV the apical segment and setae are in the process of disappearing. In many reared individuals three or fewer setae are still present, while in more well developed specimens and in many larvae from the plankton the basal segment is shortened and the apical article and setae are missing entirely. In subsequent stages the distal portion, representing the exopod, expands and in the final stage assumes the paddle-shaped form of the scaphognathite.

Maxilliped 1 first appears in well developed stage IV individuals as a low bud posterior to the base of maxilla 2. In subsequent stages it becomes larger and shows signs of differentiation into an outer lobe. In the final stage maxilliped 1 is a relatively short, finger-like process with a lobe representing the epipodite on the outer side near the base.

Maxillipeds 2 and 3 each consist of five segments, and lack an exopod. The second segment of maxilliped 3 has a slight bump laterally representing the presumptive exopod bud, which shows no further differentiation during development. The proximal portion of the second segment of maxilliped 2 develops a slight lateral protuberance in a late stage; in the final stage this appears as a small rounded exopod bud.

Pereiopods 1-3 are well developed in stage I. Pereiopod 3 is only slightly longer than pereiopod 2. The exopods of pereiopods 1-2 respectively bear 7½-8 and 8 pairs of natatory setae. This number was not found to vary and is a useful diagnostic character. The exopod of pereiopod 3 is a small bud, which in stage II becomes an elongated, non-setose rudiment. In the following stage it is well developed with 6½-7 pairs of natatory setae. Pereiopod 4 is indicated in stage I as a minute bud at the base of the abdomen. In stage II it becomes an elongated bud about twice the length of the latter, with the exopod indicated as a small fold dorsally. In stage III pereiopod 4 is a more or less distinctly segmented rudiment with a short exopod bud. The exopod in the next stage is elongated and in well developed individuals may bear a few pairs of natatory setae. The number of pairs of natatory setae on the exopods increases, but not uniformly, at each ecdysis. The number for various phyllosoma stages is given in Table 4. Pereiopod 5 first appears in stage II as a small bud at the base of the abdomen, and by IV is an elongated rudiment at least half the length of the latter. In subsequent stages it becomes segmented and extends to or slightly beyond the end of the telson. A relatively short coxal spine with accessory seta is present on maxilliped 3 and persiopods 1-3 in stage I, and appears on pereiopods 4 and 5 as they become differentiated. The coxal spines persist throughout larval development. The dactyls at all stages are short and claw-like.

The uropods are first indicated in stage III as swellings on each side of the abdomen, and become bilobed rudiments in stage IV. In subsequent stages the uropods become well developed and oval in outline. In the final stage the outer ramus, with indications of articulation at the base, is slightly longer than the inner and extends beyond the posterior margin of the telson.

The pleopods appear in well developed stage IV individuals as four pairs of low folds, which in subsequent stages become short, biramous rudiments. In the final stage they are elongated, with little or no indication of articulation to the protopodite; the endopod is slightly longer than the exopod, with the incipient appendix interna indicated only as a faint swelling on the medial side.

Well developed gill buds are present only in the final stage; their distribution is given in Table 5.

Description of Stages

The following descriptions and illustrations are based on the full sequence of seven stages reared in the laboratory.

Stage I (fig. 7). Length 1.5-1.7 mm. Fore-body slightly wider than long, nearly twice width of hind-body. Abdomen slightly more than 1/3 length of hind-body, narrow, not tapering much posteriorly; a short spine and three small setae at each postero-lateral angle. Eye not stalked, about as long as antennule. Latter unsegmented, with three

terminal aesthetascs plus a small spine or seta at inner distal angle; a small seta on medial side slightly beyond middle of its length. Antenna uniramous, about 1/5 length of antennule; a small seta on each side near distal end. Maxilla 1 biramous, without palp; coxal endite with one stout, elongated terminal seta plus a shorter, similar seta and two small spines or setae; basal endite with two strong terminal teeth plus two small subterminal spines or setae and a seta proximally near anterior margin. Maxilla 2 consisting of an elongated basal segment and a small, narrow apical article bearing three long, plumose setae; anterior margin of basal segment with a minute seta distally. Maxilliped 1 not indicated. Maxillipeds 2 and 3 each with five segments, without exopod; second segment of maxilliped 3 with slight bump on outer side representing presumptive exopod bud. Pereiopods 1-3 well developed; pereiopod 3 not much longer than pereiopod 2. Pereiopod 4 a minute bud at base of abdomen; pereiopod 5 not indicated. Exopods of pereiopods 1 and 2 respectively with 7½-8 and 8 pairs of natatory setae; exopod of pereiopod 3 a small bud. Dactyls relatively short and claw-like. Maxilliped 3 and pereiopods 1-3 with a relatively short coxal spine with an accessory seta at base. Pleopods and uropods not indicated.

State II (fig. 8). Length 2.2-2.4 mm. Fore-body about as wide as long, not quite twice width of hind-body. Eye stalked; eye and stalk about 1.2 times length of antennule. Latter with terminal tuft of four aesthetascs plus

a small seta at outer distal angle; and additional tuft of two aesthetascs proximally. Inner flagellum indicated as small protuberance with short seta at tip. Antenna about 1/3 length of antennule. Exopods of pereiopods 1-2 respectively with 8½-9 pairs of natatory setae; exopod of pereiopod 3 an elongated rudiment without setae. Pereiopod 4 an elongated bud about twice length of abdomen; exopod indicated as fold dorsally. Pereiopod 5 a small bud at base of abdomen.

Stage III (fig. 9). Length 2.9-3.4 mm. Fore-body slightly longer than wide, 1.8-1.9 times wider than hind-body; outline assuming shape of a circle drawn out obtusely anteriorly and posteriorly. Abdomen not much broader at base. Eye and stalk 1.3-1.4 times length of antennule. Peduncular portion of antennule in some specimens with faint indication of a division; outer flagellum not distinctly marked off from peduncle, with an additional tuft of one or two aesthetascs; inner flagellum a distinct cylindrical process. Antenna slightly more than 1/3 length of antennule. Exopods of pereiopods 1-2 respectively with 10-10½ and 11 pairs of natatory setae; exopod of pereiopod 3 well developed, with 6½-7 pairs of setae. Pereiopod 4 an elongated rudiment roughly five times length of abdomen, consisting of six more or less distinct segments; a minute spine indicated on coxal segment; exopod a small bud. Pereiopod 5 a short bud at base of abdomen. Uropods indicated as swellings on each side of abdomen.

Stage IV (fig. 10). Length 3.9-4.8 mm. Fore-body more or less subcircular in outline, not much longer than wide, 1.8-1.9 times wider than hind-body. Abdomen short, broader at base; posterior margin of telson more or less straight; posterolateral spines short. Eye and stalk about 1.4 times length of antennule. Antennular peduncle with two distinct segments, proximal twice length of distal; outer flagellum distinctly marked off from peduncular portion, with one or two additional tufts of aesthetascs. Antenna not quite half length of antennule, with a small process laterally. Basal endite of maxilla 1 with a third, somewhat smaller terminal tooth. Maxilla 2 in process of losing apical article and setae; basal segment somewhat shortened; in many individuals three or fewer setae still present; in the most well developed specimens setae absent. Maxilliped 1 not indicated. Exopods of pereiopods 1-3 respectively with 12-13, 12-13, and 9-11 pairs of natatory setae. Pereiopod 4 at least 1/2 length of pereiopod 3; exopod in most individuals an elongated rudiment without setae; in the most advanced individuals with a few setae distally. Pereiopod 5 an elongated bud at least 1/2 length of abdomen. Uropods small, shallowly cleft rudiments. Pleopods in most individuals not indicated; in the most well developed specimens faintly indicated as folds in cuticle.

Stage V (fig. 11). Length 4.9-6.6 mm. Fore-body subcircular in outline, slightly longer than wide, 1.7-1.8 times wider than hind-body. Abdomen somewhat less than

1/2 length of hind-body, broad at base, forming tapering continuation of latter; posterolateral spines of telson small, inconspicuous. Eye and stalk about 1.4 times length of antennule. Antennular peduncle with a third more or less distinct segment; inner flagellum roughly 2/3 length of outer flagellum. Antenna extending about to end of antennular peduncle, with a small, distinct triangular process laterally; indications of a division distal to process. Basal endite of maxilla 1 with three subequal teeth, occasionally with a fourth. Maxilla 2 a single segment, beginning to expand distally. Maxilliped 1 a low rounded bud posterior to base of maxilla 2. Exopods of pereiopods 1-3 respectively with 14-15, 14-16 and 12-13 pairs of natatory setae. Exopod of pereiopod 4 well developed, with 5-8 pairs of natatory setae. Pereiopod 5 an elongated rudiment extending to or slightly beyond end of telson; coxal segment clearly demarcated; remainder with indications of division. Uropods expanded, biramous rudiments not extending to end of telson. Pleopods four pairs of low, distinct buds, in the most well developed specimens with trace of bifurcation at tip.

Stage VI (subfinal) (fig. 12). Length 5.6-8.5 mm. Fore-body subcircular in outline, about 1.1 times longer than wide, 1.6-1.7 times wider than hind-body. Abdomen about 1/2 length of hind-body; some segmentation dorsally at midline. Eye and stalk 1.4-1.5 times length of antennule. Antenna somewhat broader, extending slightly beyond

end of antennular peduncle. Distal portion of maxilla 2 expanded anteriorly and posteriorly. Maxilliped 1 a conical bud showing indications of differentiation into an outer lobe. Second segment of maxilliped 2 with slight protuberance laterally representing incipient exopod bud. Exopods of pereiopods 1-4 respectively with 15-16, 16-17, 14-15 and 10-11 pairs of natatory setae. Pereiopod 5 consisting of five more or less distinct segments, extending somewhat beyond end of telson; coxal segment with a small spine. Uropods well developed, oval; outer ramus not much longer than inner, extending slightly beyond end of telson. Pleopods short, distinctly biramous rudiments; rami subequal in length. Small, incompletely developed gill buds indicated only in the most well developed individuals.

Stage VII (final) (fig. 13). Length 8.3-10.2 mm. Fore-body subcircular in outline, about 1.1 times longer than wide, 1.5-1.6 times wider than hind-body. Abdomen well developed, roughly 4/5 length of hind-body, broad at base, tapering posteriorly; segments marked off dorsally near midline; postero-lateral spines of telson small, inconspicuous, not extending to level of posterior margin of telson at midline. Eye and stalk 1.3-1.5 times length of antennule. Length of segments of antennular peduncle in approximate ratio 100:85:63 from proximal to distal. Inner antennular flagellum about as long as outer flagellum. Antenna broad, shorter than antennule; an articulation indicated distal to lateral process; distomedial margin of

antenna shallowly crenulate, with a few small setae at intervals. Coxal endite of maxilla 1 with two stout, elongated terminal setae plus smaller terminal and subterminal spines or setae; basal endite with three strong terminal teeth plus a few smaller spines or setae. Distal portion of maxilla 2 expanded in paddle-shaped form of scaphognathite. Maxilliped 1 a short, finger-like process with a posteriorly directed lobe representing epipodite. Second segment of maxilliped 2 with a small, rounded exopod bud. Presumptive exopod bud of maxilliped 3 showing no further differentiation. Exopods of pereiopods 1-4 respectively with 17-18, 18, 16-17 and 12-13 pairs of natatory setae. Pereiopod 5 a rudiment consisting of five distinct segments, extending to or slightly beyond end of telson. All dactyls short and claw-like. Maxilliped 3 and pereiopods 1-5 with a coxal spine. Uropods well developed; outer ramus, with indications of articulation at base, slightly longer than inner, extending beyond posterior margin of telson. Pleopods elongated, with little or no indication of articulation to protopodite; endopod slightly longer than exopod, with faint swelling medially representing incipient appendix interna. Gill buds present.

Coloration of reared phyllosomas. Orange red chromatophores are distributed in stage I, as indicated in fig. 7, on the eye, on either side of the median eye near the base of the antennule, near the base of each lobe of the lower lip, near the edge of the hind-body anterior to the bases

TABLE 4

NUMBER OF PAIRS OF NATATORY SETAE ON THE EXOPODS OF PEREIOPODS 1-4 IN VARIOUS REARED PHYLLOSOMA STAGES OF *SCYLLARUS AMERICANUS*

Stage	TL (mm)	P. 1	P. 2	P. 3	P. 4
I	1.5-1.7	7½-8	8	ex.bud	
II	2.2-2.4	8½-9	9	ex.bud	
III	2.9-3.4	10-10½	11	6½-7	ex.bud
IV	3.9-4.8	12-13	12-13	9-11	0-3
V	4.9-6.6	14-15	14-16	12-13	5-8
VI (subfinal)	5.6-8.5	15-16	16-17	14-15	10-11
VI (final)	8.5-9.0	16-17	17-18	15-16	11-12
VII (final)	8.3-10.2	17-18	18	16-17	12-13

TABLE 5

DISTRIBUTION OF GILL BUDS IN THE FINAL PHYLLOSOMA OF *SCYLLARUS AMERICANUS*

		Podobranch	Arthrobranch	Pleurobranch	Epipodite
Maxilliped	2	0	0	0	0
"	3	1	1	1	1
Pereiopod	1	1	1	1	1
"	2	1	1	2	1
"	3	1	1	2	1
"	4	1	1	2	1
"	5	0	0	1	0

of maxillipeds 2-3 and pereiopods 1-3, and in the midline of the hind-body near the base of the abdomen. Chromatophores are located on the appendages near the distal end of the third and fourth segments of maxilliped 2; near the presumptive exopod bud, and at the distal end of the second, third and fourth segments of maxilliped 3; and at the distal end of the basis, ischiomerus, carpus and propodus of pereiopods 1-3.

In subsequent stages two or three additional chromatophores are present medially on each eye and several appear at various points on the hind-body. A few chromatophores appear on the coxal segment of pereiopods 1-4, and numerous small ones become distributed along the length of the basis, ischiomerus, carpus and propodus of these legs. In a late stage small chromatophores may be present at the distal end of the first four segments of pereiopod 5. Inconspicuous ones may appear on the antenna and near the base of the maxillae. Many of the chromatophores noted above are inconspicuous even in living specimens and fade rapidly upon the death or preservation of the larva.

Discussion. The illustrated stages represent more or less the average development attained by laboratory reared individuals which reached the final phyllosoma in stage VII. The few larvae in the experiments which became final phyllosomas in the sixth stage were somewhat more advanced at stage IV and the subfinal stage of development was attained at the next ecdysis. I believe a similar development to

occur in some larvae from the plankton, many of which have the outer process of the antenna faintly indicated in stage III. In stage IV maxilliped 1 may be indicated as a low bud, the form of maxilla 2 may approach that illustrated for stage V, the pleopods may be low, crescent-shaped buds, pereiopod 5 may be nearly as long as the abdomen, and the exopod of pereiopod 4 may bear a few pairs of natatory setae.

The number of pairs of setae on the exopods of pereiopods 3 and 4 appears to be a useful character for distinguishing between advanced stage IV larvae and poorly developed stage V individuals. In reared stage V larvae the minimum number of setae pairs on the exopods of pereiopods 3 and 4 was 12 and 5 respectively. In stage IV the corresponding maximum number was 11 and 3. Among planktonic larvae it appears that the exopod of pereiopod 4 in an occasional stage IV specimen may bear up to 5 pairs of setae. In most planktonic larvae which can be assigned with certainty to stage V the exopod of pereiopod 4 bears 7 or 8 pairs of setae.

There is a gradation among planktonic specimens between stages V and VI. It seems likely that the more advanced stage IV individuals attain a development in the fifth stage at least intermediate between the illustrated stages V and VI, and that the final phyllosoma stage of development is reached in stage VI. The number of pairs of setae on the exopods may provide some indication, but I have found no reliable characters for determining with certainty whether

larvae in what may be considered the subfinal stage represent stage V or VI, or whether final phyllosomas are in stage VI or VII.

The phyllosomas from the northwestern coast of Cuba reported as _Scyllarus_ sp. by Baisre (1966) undoubtedly belong to _S_. _americanus_, as he thought was probable. Baisre found larvae of this species in coastal waters, but never far offshore in oceanic waters. I find a similar distribution in the present study. Larvae of _S_. _americanus_ were the most common phyllosoma in waters of the Tortugas Shelf, at stations over depths ranging from 3 to 26 fathoms, but were not found in numerous plankton samples from the Straits of Florida and other offshore areas in the Atlantic. Rearing experiments indicate that larvae of this species can develop over a fairly wide range of salinity. In view of the relatively inshore distribution of both adult and larvae, it seems probable that in some areas in nature hatching and possibly the entire larval development take place in waters subject to marked salinity fluctuations.

Robinson and Dimitriou (1963a, b) found phyllosoma larvae on the Tortugas Shelf in every month of the year except January, with the greatest abundance in the spring and summer, although the average number taken per tow was never high. The seasonal distribution of the various stages of _S_. _americanus_ which I identified among their collection is given in Table 6. Because of the sampling procedures, these data do not necessarily reflect the

relative numerical abundance of the various stages. None of the specimens examined were taken during the months November-January. Most of Baisre's material was collected during March-June, but he found small numbers of stage I and II in late November and early December. It appears, therefore, that at least in the southern part of the range some spawning of S. americanus may occur throughout the year, with a peak in the spring and summer. Ovigerous females are found in the Miami area as early as January, and on the west coast of Florida during February to May (Sims, 1966b). Williams (1965) recorded ovigerous females from southern Florida in September.

The rearing experiments indicate that complete larval development at 20°C might require 40 to 50 days. Individuals hatched during the winter would therefore have a longer larval life than those hatched in the late spring or summer. Surface temperatures on the Tortugas Shelf during July and August are often 30°C or higher (Jones et al., 1963). Phyllosomas of S. americanus hatched at that time might develop to postlarvae in less than one month.

Baisre's samples included a total of 336 stage I phyllosomas but only 34 in stage II. Results of the rearing experiments in the present investigation do not support his suggestion that this may indicate a high mortality of the larva at the first ecdysis, although in nature there undoubtedly is a progressive mortality from predation and other factors.

TABLE 6

SEASONAL DISTRIBUTION OF PHYLLOSOMA LARVAE OF *SCYLLARUS AMERICANUS* IN WATERS OF THE TORTUGAS SHELF

Date		Number of larvae by stage						
		I	II	III	IV	V	Subfinal	Final
Feb.	1962	1		2				
March	1962	6	2	5	7	1	5	3
April	1962	9	16	29	20	6	14	11
May	1961	15			1	1	5	14
	1962	13	15	10	15	10	10	5
June	1961				2	1	1	4
	1962		1	2	3	2	3	9
July	1960						3	3
	1961				1		4	5
Aug.	1960		1	2	2	2	8	18
Sept.	1961	2	5	11	6	1	4	1
Oct.	1960						1	2
		46	40	61	57	24	58	75

The Postlarva of Scyllarus americanus

(Figures 14, 15)

Metamorphosis occurred at night. The postlarvae are about three-fourths the length of the final phyllosoma as a result of the fusion at metamorphosis of the cephalic shield with the thorax to form the cephalothorax. The chitinous exoskeleton is not calcified. Numerous small, red brown chromatophores were distributed over the entire dorsal surface. Red, apparently larval chromatophores were still present on the pereiopods, the eyes, and the basal article of the antennule. The median eye was still visible in fresh specimens. Short, nonsetose vestiges of the larval exopods are present at the outer distal end of the basis of pereiopods 1-4. The pleopods (fig. 15, B) have the form characteristic of the postlarval stage. Both rami are well developed and fringed with plumose setae; the endopod bears a cylindrical appendix interna or coupling process provided with several minute hooks at its inner distal end.

Measurements. TL 6.4-7.0 mm; length of carapace in midline 2.6-2.8 mm; width of carapace at anterolateral angles 3.0 mm; length of abdomen to tip of telson 3.8-4.2 mm.

Description. Maximum width of carapace at anterolateral angles; latter not projecting much anteriorly. Middorsal ridge of carapace with a cardiac eminence and a sharper, more elevated gastric eminence; pregastric eminence

scarcely indicated; a small, rounded rostral protuberance. A dentate lateral carina on each side of carapace, interrupted behind orbit. Lateral border of carapace with a notch behind eye, followed posteriorly by a broad, shallow notch, dentate behind latter. Posterior margin of carapace acutely notched in midline. Distal article of antenna with anterior border cut into five rounded lobes; a small lobe medially. Lateral margin of proximal movable article of antenna shallowly dentate, not cut into prominent teeth; anterolateral corner not acute; ridge running to latter obscure. Sternum behind base of pereiopod 5 not projected in prominent spine. Abdominal tergites devoid of sculpture. Segments 2-5 with an elevated carina in midline. Segments 1-3 with a median notch at posterodorsal margin; segment 4 shallowly indented. Pleura of segment 2 somewhat angular distally but not terminating in a distinct, posteriorly directed spiniform tip; pleura of segments 3-5 more or less obtuse distally.

Discussion. Postlarvae of Scyllarus have been studied by Boas (1880), Sarato (1885), Bouvier (1913, 1915, 1917, 1940), Fedele (1926) and Alikunhi (1949), among others. The postlarval stage was termed the "natant stage" by Boas and was given the generic name "Nisto" by Sarato. Gurney (1942) remarked that the first postlarval stage of Scyllaridea "has received undue notoriety, since it actually differs less from the adult than many other first postlarval stages."

Fedele obtained the postlarva of S. arctus (L.) from metamorphosis of the last phyllosoma stage in the laboratory. During several days of observation the animal exhibited the typical reptant behavior of the adult and was never seen to swim by the pleopods in the sense supposed by Boas. The question of the habits of the postlarva was discussed by Dawydoff (1929), who accepted Fedele's observation that the so-called natant stage does not swim. Alikunhi (1949) studied the postlarval stages of two species of Scyllarus obtained through metamorphosis of the final larva in the laboratory, but the results of his investigations have been published only as a brief abstract.

In the present study postlarvae of S. americanus when disturbed from behind would sometimes rise off the bottom and swim forward obliquely toward the surface by vigorous action of the pleopods, which are coupled in pairs by their appendices internae. They quickly sank back to rest again on the bottom, however, and there is no doubt that they are essentially bottom-dwelling forms. The limited ability to swim in short spurts by means of the pleopods conceivably might aid in the selection of a suitable substrate for settling following metamorphosis.

A small (TL 18.7 mm), undoubtedly immature scyllarid dredged at a depth of 86 fathoms near Block Island, off the coast of Rhode Island, was described by Smith (1881) under the name Arctus depressus. He suggested that it might possibly prove to be the young of Arctus americanus

Smith (= *Scyllarus americanus*), though he considered this very improbable because the specimen was "half as long as ordinary specimens of *A. Americanus*." In Smith's specimen, which I have examined, the edges of the sternum "terminate posteriorly, back of and below the base of the fifth leg, in a conspicuous spine, directed backward." As he pointed out, these sternal spines may disappear in the adult.

Bouvier (1915, 1917) suggested that it might be possible to regard *Arctus depressus* as the second postlarval stage of *Scyllarus americanus*. He (1925: 450, pl. 8, fig. 2) described as the postlarva of *S. americanus* a scyllarid 16 mm in length which was dredged at a depth of 80 fathoms off Sand Key, Florida. According to his description, this specimen possesses a spine on the sternum at the base of the fifth leg and a spiniform point at the tip of the pleura of abdominal segments 2-4. Bouvier noted that *Arctus depressus* differed from his specimen in having less prominent cardiac and gastric eminences and pleural points only on the second abdominal segment, in addition to its somewhat greater size.

In my opinion the absence in the postlarvae obtained in the present study of both posterior sternal spines and distinct spiniform tips on any of the abdominal pleurae, as well as the small size of the animals, precludes any possibility that either Bouvier's specimen or the *Arctus depressus* of Smith are postlarval stages of *S. americanus*. The identity of the latter specimens is discussed in the present work under *Scyllarus nearctus*.

B. *Scyllarus nearctus* Holthuis

Materials and methods. Two ovigerous females approximately 24 mm in carapace length and two smaller males were collected by R/V GERDA on 26 Jan. 1966 at 25° 11'N, 80°10'W, near the edge of the Straits of Florida off Key Largo. The specimens were taken in a 10' otter trawl at a depth of about 100 meters.

They were returned to the laboratory on the following day and were placed in a 2½-gallon aquarium provided with running sea water and a layer of sand on the bottom. The water temperature was 18-20°C. On the next day each female tore off all her eggs, which were in a relatively advanced stage of development. Attempts to hatch some eggs in compartments of plastic trays on a shaker were unsuccessful.

On 16 Feb. both females were found to bear a fresh brood of eggs, which could have been deposited up to three days before. Recently deposited eggs were bright yellow and measured 0.37-0.43 mm in diameter. Shortly before hatching the eggs were more or less spherical and 0.50-0.54 mm in diameter. A large hatching occurred in the early morning of 7 March. The newly hatched larvae were in the first phyllosoma stage; no free-swimming earlier stages were observed. Water temperature in the aquarium at time of hatching was 21°C; salinity was 33.4 °/oo.

The eggs carried by the second female hatched on 13 March, and on 21 March both females were again found to be gravid. A hatching occurred on 7 April. On 10 April the same female was discovered to have deposited another fresh brood of eggs. Larvae from three different broods were reared under various conditions. One of the females is deposited in the Invertebrate Museum of this Institute (Acc. No. 32.3587).

About 25 phyllosomas from the plankton, ranging from 3.1 mm in length to the final stage, were determined by comparison with reared material to be larvae of _Scyllarus nearctus_. The collection data are given in Table 7. Most were taken in the Straits of Florida. A final phyllosoma 24.4 mm in length was recovered in excellent condition from the stomach of the lancetfish _Alepisaurus ferox_ Lowe, taken in the central Gulf of Mexico. Two final phyllosomas collected in the Straits of Florida in 1959 were placed in compartments of a plastic tray and were returned alive to the laboratory by Dr. A. J. Provenzano, Jr. They were held at 20°C. Metamorphosis of both specimens occurred within a few days. The postlarvae were preserved together with the phyllosoma exuviae. Four final phyllosomas were taken in a 10' IKMT on 6 April 1968 at P-641, in the Straits of Florida opposite Miami Beach. They were returned alive to the laboratory by Mr. John Shoup and were held in $\frac{1}{2}$-gallon glass jars at a temperature of 23-25°C. Metamorphosis of one specimen occurred on the night of 9 April; another

TABLE 7

LIST OF STATIONS AT WHICH PHYLLOSOMAS OF *SCYLLARUS NEARCTUS* WERE TAKEN

Station	Date (D/M/Y)	Position		Time	Gear	Gear depth(m)	No. of larvae	TL mm
		Lat. N	Long. W					
G-96	9/V/63	$25^{\circ}31-35'$	$79^{\circ}51-56'$	1237-1435	6'IKMT	120-130	2	final
G-204	18/I/64	$23^{\circ}24-40'$	$82^{\circ}54'-83^{\circ}17'$	1240-1535	6'IKMT	800-900	1	8.2
G-212	20/I/64	$23^{\circ}33.5-43'$	$82^{\circ}31-37'$	0530-0830	6'IKMT	860	1	11.2
G-213	20/I/64	$23^{\circ}35-43'$	$82^{\circ}40.5-49'$	1105-1400	6'IKMT	777	2	8.7,12.4
G-505	4/II/65	$25^{\circ}39-53'$	$80^{\circ}00-01'$	1940-2020	2m plank. net	9	1	8.3
P-641	6/IV/68	$25^{\circ}47'$	80°	2120-2245	10'IKMT	100-150	4	final
SL 109 3	27/I/64	$25^{\circ}45'$	$79^{\circ}57'$	1250-1320	3/4m plank. net	103	1	12.0
SL 110 2	29/III/64	$25^{\circ}37'$	$80^{\circ}02'$	1135-1205	3/4m plank. net	40	1	4.2
SL 115 4	31/III/64	$25^{\circ}35'$	$80^{\circ}02'$	2330-2400	3/4m plank. net	109	1	8.8
TURSIOPS-245	1/III/66	$25^{\circ}35-36'$	$80^{\circ}03-04'$	2120-2150	2m plank. net	10?	1	7.0
TURSIOPS-246	1/III/66	$25^{\circ}35-36'$	$80^{\circ}00-02'$	2215-2258	2m plank. net	30?	1	3.1
M/V MILINAR	V/57	Central Gulf of Mexico		--	stomach of *Alepisaurus*		1	24.4
10 mi. E. Miami	13/IV/59	$25^{\circ}35-45'$	$79^{\circ}56-58'$	1130-1200	3'IKMT	100	1	6.7
"	"	"	"	1330-1400	6'IKMT	130	2	8.3,17.0
"	"	"	"	1400-1415	6'IKMT	160	3	6.8-15.3
"	"	"	"	1500-1530	6'IKMT	190	2	8.4,17.0
"	"	"	"	1540-1620	6'IKMT	200	1	11.5

phyllosoma metamorphosed on 14 April. Both postlarvae died within one day after metamorphosis and were preserved. Representative reared and planktonic phyllosomas are deposited in the Invertebrate Museum of this Institute (Acc. No. 32.3596).

Results. In no instance did starved larvae molt (fig. 22). The mean survival time in days for 18 individuals at each temperature was 9.8 at 10°C, 11.8 at 15°C, 9.5 at 20°C, 7.5 at 25°C, and 3.9 at 30°C.

The results of rearing at various temperatures larvae hatched on 7 March are shown in fig. 23. These larvae were reared in bay water at salinity 33-35 °/oo. At 10°C they began dying on the fifth day; total mortality of 18 individuals occurred within 14 days. None molted. At 15°C a few larvae eventually molted to stage II after about four weeks, but none survived to the next stage. At both 20° and 25°C roughly half of the larvae reached stage V, after which mortality became appreciable. Only a few individuals survived to the eighth stage. Stage VII at 20°C was first reached 53 days after hatching, and after 42 days at 25°C. Mortality was high among larvae reared at 30°C; none survived beyond stage II.

Table 8 gives the duration of the various stages at different temperatures. At 25°C the mean durations of the first five stages were within 7 ± 1 days. That of the next two stages was somewhat greater. The total duration at 20° and 25°C through the first seven stages was respectively

TABLE 8

DURATION IN DAYS OF THE LARVAL STAGES OF *SCYLLARUS NEARCTUS* REARED AT VARIOUS TEMPERATURES

	15° C			20° C			25° C			30° C		
Stage	Mean	Range	No. of larvae	Mean	Range	No. of larvae	Mean	Range	No. of larvae	Mean	Range	No. of larvae
I	27.7	27-29	3	9.7	8-12	31	7.9	7-10	96	7.0	6-9	12
II	--	--	---	8.1	6-10	27	6.2	5-10	96	--	--	--
III				8.8	8-11	22	6.1	5-8	89			
IV				9.0	8-11	18	6.6	6-8	69			
V				10.5	8-13	13	7.6	6-11	49			
VI				10.8	9-16	6	9.5	6-14	7			
VII				17	17	1	10.5	9-12	2			

74 and 54 days, based on the values for the mean duration of each stage. The value for stage VII at 20°C is derived from only one individual.

Growth of both reared and planktonic larvae is shown in Table 9. The growth factor at the first ecdysis in the laboratory was 1.36. It was nearly the same at the next ecdysis, but declined after the third stage, although not markedly, and leveled off from stages V-VII. A steady progression in morphological development was observed through the first seven stages reared. Reared individuals in stage VIII and a single larva which reached a ninth stage showed some increase in length but little advance in morphology beyond that of a well developed stage VII larva. The morphological development of the latter corresponded more or less to planktonic phyllosomas 6.7-8.8 mm in length.

Later specimens from the plankton fell into three rather well defined stages, the last of which is the final phyllosoma. It appears therefore that the larval history of this species consists of ten phyllosoma stages. In view of the decreasing growth factor observed in the laboratory, it is possible that under favorable conditions in nature the degree of development represented by the reared stage VII might be reached at the sixth stage. In that case there would be a total of nine phyllosoma stages. Few early stages from the plankton were available for comparison with reared material. The growth factor for the last three stages from the plankton, based on a small number of individuals, was

between 1.39 and 1.57, somewhat greater than for any successive reared stages.

The total duration in the laboratory at 25°C through the first seven stages was 54 days, and the mean duration of stage VII was 10.5 days. If the duration in nature of each of the three following stages is as least as great as that observed for the reared stage VII, then slightly less than three months appears to be a minimum estimate for the total duration of larval life of S. nearctus at 25°C. The total duration would be somewhat greater if the intermolt period of the last stages increases significantly, as was observed for S. americanus in the laboratory.

The planktonic phyllosomas of S. nearctus were collected from January through May, the final phyllosomas being taken in April and May. Postlarvae were taken in late March, April and May (see Table 10). If hatching and development occur during the winter and early spring in the south Florida area, as available records of both larvae and ovigerous females indicate, the larval life might be extended to perhaps four months by the lower water temperatures prevailing at that time. Stephensen (1923), from the seasonal distribution of the various stages of S. arctus in the eastern Atlantic and Mediterranean, thought that development of that species took place "comparatively quickly," probably in a few months.

TABLE 9

GROWTH OF LARVAE OF *SCYLLARUS NEARCTUS*

Stage (reared)	Mean length mm	Number measured	Growth Factor
I	1.24	8	
II	1.69	8	1.36
III	2.33	8	1.38
IV	3.07	7	1.32
V	3.94	10	1.28
VI	5.10	8	1.29
VII	6.56	12	1.29
VIII	7.27	7	1.11
(plankton)			
IV	3.1	1	
V	4.2	1	1.35
VI	---	0	----
VII	8.0	10	----
VIII	11.8	4	1.48
IX (subfinal)	16.4	3	1.39
X (final)	25.8	3	1.57

Diagnosis of the Phyllosoma

Antennule in early stages with a relatively long medial spine; exopod of pereiopod 2 in stages I-III respectively with 5, 6 and 7-8 pairs of natatory setae. Posterolateral telson spines elongated in intermediate stages; antenna becoming slightly longer than antennule. Fore-body in later stages broadly subquadrate in outline; a prominent spine dorsally at edge of hind-body adjacent to insertion of pereiopods 1-4. Last two stages large, respectively about 15-17 and 24-27 mm in length.

Characters of the Phyllosoma

The fore-body in stage I is slightly wider than long and about 1.7 times wider than the hind-body. In subsequent stages it becomes relatively broader, being by stage VI twice the width of the hind-body. In late stages the fore-body is broadly subquadrate in outline, 1.2-1.3 times wider than long, and about 2.3 times wider than the hind-body. The posterolateral margins of the fore-body in stage I cover the anterior part of the base of maxilliped 3. By stage VII they cover the anterior portion of the base of pereiopod 1, and in the final stage cover part of the base of pereiopod 2.

The abdomen in early stages is short, narrow, and more or less parallel-sided. In stage I a short spine and three small setae are present at each posterolateral angle. At

Stage III these spines begin to become noticeably elongated, and by stage VI are about 2/3 the length of the abdomen measured in the midline; the telson is deeply concave with the tapering spines extendingly posteriorly on each side. In subsequent stages the abdomen becomes broad at the base, the posterior margin of the telson becomes rounded, and the spines become relatively shorter. In the final stage they extend slightly beyond the posterior margin of the telson at the midline. The abdomen in the final stage is about 4/5 the length of the hind-body, with the segments marked off dorsally near the midline and indicated elsewhere.

The eye in stage I is not stalked and is slightly shorter than the antennule. It becomes stalked in stage II. In intermediate and late stages the eye and stalk are about 1.5 times the length of the antennule.

The antennule in stage I has a relatively long, stout anteroventrally directed spine or seta on the medial side somewhat beyond the middle of its length. In subsequent stages this spine becomes shorter and is borne at the tip of the inner flagellum, which becomes differentiated as a short process in stage III. The inner flagellum gradually increases in length, and in the final stage is at least as long as the outer flagellum. A distinct articulation first appears in the antennular peduncle at stage VI. At that time the outer flagellum is distinctly marked off from the peduncular portion. In the following stage the peduncle consists of three more or less distinct segments, the

lengths of which in the final stage are in the approximate ratio 100:70:57 from proximal to distal.

The antenna in stage I is short and uniramous. In subsequent stages is becomes progressively longer, until by stage VII it is slightly longer than the antennule. In later stages it becomes broad and remains longer than the antennule. At stage IV a slight protuberance is indicated on the outer side of the antenna toward the proximal end. In stage V this appears as a small, distinct triangular process, which becomes larger in subsequent stages. In stage VIII a division is indicated beneath the cuticle of the antenna distal to the process. In the final stage the antenna is expanded, with incisions indicated distally beneath the cuticle.

Maxilla 1 is biramous, without palp. The coxal endite in stage I has one stout, elongated terminal seta plus a much smaller seta and a terminal spine; the basal endite has two strong terminal teeth plus two slender subterminal spines or setae and a small seta proximally near the anterior margin. The smaller terminal seta of the coxal endite becomes larger as development progresses. The basal endite acquires a third terminal tooth at stage VI. A few spines or setae are added to each endite during development.

Maxilla 2 in early stages consists of an elongated basal segment and a small, narrow apical article which usually bears four long, plumose setae. In an occasional

specimen only three setae are present. Little change occurs until the ecdysis to stage VII, at which the apical segment and setae are in the process of disappearing. In some specimens four or fewer setae are still present, while in more advanced individuals they may be missing entirely. The distal portion, representing the exopod, begins to expand in the next stage. In the final stage it is much expanded in the paddle-shaped form of the scaphognathite.

Maxilliped 1 first appears in stage VII as a low bud posterior to the base of maxilla 2. In the next two stages it becomes larger and shows indications of differentiation into an outer lobe. In the final stage it is a finger-like process with a relatively large, oval lobe on the outer side representing the epipodite.

Maxillipeds 2 and 3 each consist of five segments and lack an exopod, although the second segment of maxilliped 3 has a slight bump on the outer side representing the presumptive exopod bud. In the final stage the latter is a minute rounded protuberance. The second segment of maxilliped 2 has a small, oval exopod bud in the final stage.

Pereiopods 1-3 are well developed in stage I. Pereiopod 3 is only slightly longer than pereiopod 2. The exopods of pereiopods 1 and 2 each bear five pairs of natatory setae. This number did not vary among a number of specimens and is a useful diagnostic character. The exopod of pereiopod 3 is a small, rudimentary bud, which becomes somewhat elongated in stage II, and in stage III acquires

two or three pairs of natatory setae. Pereiopod 4 in stage I is faintly indicated as a minute bud at the base of the abdomen, which by stage IV has become an elongated, more or less distinctly segmented rudiment possessing a short exopod bud. The latter becomes elongated in stage V and may acquire a few pairs of setae. In the following stage it becomes fully functional with 5½-7 pairs of natatory setae. After the first few stages more than one pair of natatory setae is added to the exopods of pereiopods 1-2 at each ecdysis.

Pereiopod 5 is first indicated in stage III as a minute bud at the base of the abdomen. By stage VII it has become a rudiment roughly half the length of the latter, with a coxal segment and spine differentiated. In subsequent stages pereiopod 5 remains a short rudiment, never extending to the end of the telson. In the last two stages it consists of five more or less distinct segments.

A coxal spine plus accessory seta is present on maxilliped 3 and pereiopods 1-3 in stage I, and one appears on pereiopods 4 and 5 in later stages. The coxal spines persist throughout development. The dactyls of all pereiopods are short and claw-like.

At stage VI a small spine appears dorsally at the edge of the hind-body adjacent to the insertion of pereiopod 4. In the last three stages a prominent triangular, posteriorly directed spine is present dorsally adjacent to the insertion of pereiopods 1-4.

The uropods appear in stage VI as small, undifferentiated folds, which in stage VII become shallowly cleft buds. In the next stage the uropods are short, biramous rudiments, which in the final stage are well developed, rounded, and relatively short, not extending beyond the posterior margin of the telson.

The pleopods are first indicated in stage VII as low buds, which become larger in stage VIII and may show slight bifurcation at the tip. In the subfinal stage they are biramous rudiments, and in the final stage are elongated. The slender rami are widely divergent; the endopod is slightly longer than the exopod, with the incipient appendix interna indicated medially beneath the cuticle.

Gill buds are present only in the final stage. Their distribution is as in _Scyllarus americanus_.

Description of Stages

Stage I, reared (fig. 24). Length 1.18-1.27 mm.

Fore-body about 1.1 times wider than long, 1.7 times wider than hind-body. Abdomen slightly more than 1/3 length of hind-body, narrow, with a short spine and three small setae at each posterolateral angle. Eye not stalked, slightly shorter than antennule. Latter with a relatively long, stout anteroventrally directed spine or seta medially somewhat beyond middle of its length; spine extending more than half the distance from its base to tip of antennule; latter with three terminal aesthetascs plus a short seta

at inner distal angle. Antenna uniramous, short, tapering to point distally, with a small seta on each side near distal end. Maxilla 1 biramous, without palp; coxal endite with one stout, elongated terminal seta plus one much smaller seta and a small subterminal spine; basal endite with two strong terminal teeth plus two slender subterminal spines or setae, one near anterior and one near posterior margin; anterior margin with a seta proximally. Maxilla 2 consisting of an elongated basal segment and a small apical article bearing usually four long, plumose setae; anterior margin of basal segment with a small seta distally. Maxilliped 1 not indicated. Maxillipeds 2 and 3 each with five segments, without exopod; second segment of maxilliped 3 with a slight bump on outer side representing presumptive exopod bud. Pereiopods 1-3 well developed; pereiopod 3 nearly 1.1 times length of pereiopod 2, latter slightly longer than pereiopod 1; a prominent spine at outer distal end of basis, ischiomerus and carpus of pereiopods 1-3; dactyls claw-like. Pereiopods 1-2 each with exopod bearing five pairs of natatory setae; exopod of pereiopod 3 only a small bud. Pereiopod 4 indicated as minute bud at base of abdomen. Maxilliped 3 and pereiopods 1-3 with a coxal spine plus accessory seta.

Stage II, reared (fig. 25). Length 1.60-1.75 mm.

Fore-body slightly wider than long, 1.7-1.8 times wider than hind-body. Spines at posterolateral angles of abdomen somewhat longer. Eye stalked; eye and stalk longer

than antennule. Latter with terminal tuft of four aesthetascs; an additional aesthetasc proximal to latter and a seta at outer distal angle; spine on medial side of antennule with a small seta near base. Antenna nearly 1/2 length of antennule. Exopods of pereiopods 1-2 each with six pairs of natatory setae; exopod of pereiopod 3 a relatively short rudiment without setae. Pereiopod 4 a bud about 1/2 length of abdomen. Pereiopod 5 not indicated.

Stage III, reared (fig. 26). Length 2.2-2.5 mm. Fore-body slightly wider than long, about 1.8 times wider than hind-body. Inner flagellum of antennule becoming differentiated as protuberance on medial side, with spine and seta at tip. Antenna 1/2 to 2/3 length of antennule. Pereiopod 2 slightly longer than pereiopods 1 and 3. Exopod of pereiopods 1-2 respectively with 7 and 7-7½ pairs of natatory setae; exopod of pereiopod 3 elongated, with 0-3, in most specimens 2, pairs of setae. Pereiopod 4 an elongated rudiment 2-3 times length of abdomen, with small spine distally; exopod indicated as small fold dorsally; coxal spine beginning to differentiate. Pereiopod 5 indicated as minute bud at base of abdomen.

Stage IV, reared (fig. 27). Length 2.7-3.3 mm. Fore-body about as long as broad, 1.8-1.9 times wider than hind-body; posterolateral margins covering base of maxilliped 3. Abdomen still narrow, about 1/3 length of hind-body; posterolateral spines distinctly elongated. Eye and stalk 1.4-1.5 times length of antennule. Latter with two tufts

of two aesthetascs each proximal to terminal tuft. Antenna slender, nearly 4/5 length of antennule; incipient outer process indicated in better developed individuals as faint protuberance on outer side toward proximal end. Exopods of pereiopods 1-3 respectively with 9, 9 and 5-6 pairs of natatory setae. Pereiopod 4 consisting of six distinct segments, roughly 1/2 length of pereiopod 3; coxal spine present; exopod a short bud without setae. Pereiopod 5 a small bud at base of abdomen.

Stage V, reared (fig. 28). Length 3.6-4.3 mm. Posterolateral spines of abdomen, measured from posterior end of abdomen in midline to tip of spine, about 2/3 length of abdomen measured in midline. Eye and stalk 1.5-1.6 times length of antennule. Inner antennular flagellum tapering distally; spine or seta at distal end shorter than in previous stages; outer flagellum not marked off from peduncular portion; latter not distinctly segmented. Antenna slightly shorter than antennule, with a distinct, slender triangular process on outer side of proximal portion. Exopods of pereiopods 1-3 respectively with 10-11½, 11-12½, and 7-9 pairs of natatory setae. Pereiopod 4 well developed, somewhat shorter than pereiopod 3; exopod elongated, with 0-2½ pairs of natatory setae. Pereiopod 5 a somewhat elongated bud less than 1/2 length of abdomen, tapering to point distally. Uropods in some individuals indicated as faint swellings at side of abdomen.

Stage VI, reared (fig. 29). Length 4.7-5.7 mm. Fore-body not much broader than long, about twice width of hind-body. Abdomen little developed. Telson concave behind, with a rigid, broad-based, tapering spine forming an extension at each posterolateral angle; spine about 2/3 length of abdomen measured in midline. Eye and stalk 1.4-1.5 times length of antennule. Outer flagellum of antennule marked off from peduncular portion; latter with two distinct segments; inner flagellum roughly 1/2 length of outer flagellum, its terminal seta much reduced in size. Antenna slender, as long as or only slightly shorter than antennule; outer process longer than before, slender, tapering to point. Coxal endite of maxilla one with one stout, elongated terminal seta plus a similar but somewhat smaller seta and a few smaller spines or setae; basal endite with a third terminal tooth. Maxilla 2 little changed. Maxilliped 1 not indicated. Exopods of pereiopods 1-4 respectively with 13-14, 13-14½, 10-11, and 5½-7 pairs of natatory setae. Pereiopod 5 roughly 1/2 length of abdomen, tapering distally to small pointed spine; small coxal spine present. Edge of hind-body adjacent to insertion of pereiopod 4 with a small triangular spine dorsally. Uropods small, undifferentiated folds. Pleopods not indicated.

Stage VII, reared (fig. 30). Length 5.4-8.1 mm. Fore-body slightly broader than long, more than twice width of hind-body; posterolateral margins covering anterior part of base of pereiopod 1. Abdomen broader at base. Antennular

peduncle with three distinct segments, proximal somewhat the longest. Antenna slender, slightly longer than antennule, with a few small setae at intervals along distal margins. Maxilla 2 with apical segment and terminal setae in process of reduction or missing entirely. Maxilliped 1 indicated in well developed individuals as a very low bud. Exopods of pereiopods 1-4 respectively with 15-18, 16-18, 13-16 and 9-13 pairs of natatory setae. Pereiopod 5 more than 1/2 length of abdomen, with a prominent coxal spine. Edge of hind-body adjacent to insertion of pereiopods 3-4 with a spine dorsally. Uropods small, shallowly cleft buds. Pleopods indicated for first time as four pairs of low, undifferentiated buds.

Stage VIII, plankton (fig. 31). Length 11.2-12.4 mm. Fore-body broadly subquadrate in outline, about 1.2 times wider than long and 2.3 times wider than hind-body; posterolateral margins covering base of pereiopod 1. Abdomen more than 1/3 length of hind-body, broad at base, tapering posteriorly. Posterolateral spines of telson relatively shorter than in previous stage, less than 1/3 length of abdomen. Eye and stalk about 1.5 times length of antennule. Antenna longer than antennule, with indications of a division distal to outer process; latter elongate, tapering to point. Maxilla 2 without setae; distal portion beginning to expand. Maxilliped 1 a short, conical bud. Exopods of pereiopods 1-4 respectively with 21-23, 22-24, 18-20 and 16-17 pairs of natatory setae. Pereiopod 5 a rudiment not

extending to end of uropods; coxal segment more or less clearly demarcated; remainder showing indistinct division. Maxilliped 3 and pereiopods 1-5 with a coxal spine plus accessory seta. Edge of hind-body adjacent to insertion of pereiopods 1-4 dorsally with a prominent triangular, posteriorly directed spine. Uropods short, biramous rudiments. Pleopods somewhat elongated buds, in the largest specimen shallowly cleft at tip.

Stage IX (subfinal), plankton (fig. 32). Length 15.3-17.0 mm. Fore-body 1.2-1.3 times wider than long, 2.3-2.4 times wider than hind-body. Abdomen about 1/2 length of hind-body, showing some segmentation dorsally at midline. Posterior margin of telson rounded in midline; posterolateral spines prominent but shorter than before. Inner flagellum of antennule as long as outer flagellum. Antenna longer than antennule, becoming broad at base. Distal portion of maxilla 2 somewhat expanded. Maxilliped 1 a bud with indications of a lobe laterally. Exopods of pereiopods 1-4 respectively with 25-26, 26-27, 23-25 and 20-21 pairs of natatory setae. Pereiopod 5 not extending to posterior end of uropods; coxal segment clearly demarcated, remainder incompletely divided into four segments; distal end of second segment with two small, sharp spines, one laterally, the other dorsally. Uropods short, rounded, not extending to posterior margin of telson. Pleopods biramous rudiments; inner ramus slightly the longer. No gill buds.

Stage X (final), stomach of Alepisaurus (fig. 33) and plankton. Length 24.4-26.5 mm. Fore-body broadly subquadrate in outline, about 1.25 times wider than long, 2.3 times wider than hind-body; posterolateral margins covering part of base of pereiopod 2. Abdomen well developed, about 4/5 length of hind-body; segments marked off dorsally near midline, indicated beneath cuticle elsewhere. Posterolateral spines of telson much less conspicuous than in preceding stages, but extending slightly beyond level of posterior margin of telson in midline. Eye and stalk 1.5 times length of antennule. Length of segments of antennular peduncle in approximate ratio 100:70:57 from proximal to distal. Inner antennular flagellum slightly longer than outer flagellum; distomedial portion of latter with numerous aesthetascs. Antenna broad, slightly longer than antennule; lateral process quite broad at base, tapering to point distally; a division in antenna distal to process; another indicated beneath cuticle near base of antenna; distal portion of medial margin shallowly crenulate; incisions visible in tissue beneath cuticle. Coxal endite of maxilla 1 with two stout, elongated terminal setae plus several smaller terminal and subterminal spines or setae; basal endite with three strong terminal teeth plus a few smaller spines or setae. Distal portion of maxilla 2 much expanded in paddle-shaped form of scaphognathite. Maxilliped 1 a finger-like process with a relatively large oval lobe laterally representing epipodite. Second segment of maxilliped 2 with a

small, oval exopod bud. Second segment of maxilliped 3 with a minute rounded protuberance representing exopod bud. Pereiopods 1-4 with a strong spine at outer distal end of basis, ischiomerus and carpus, in addition to numerous smaller spines or setae. Exopods of pereiopods 1-4 respectively with 29, 28, 25 and 23 pairs of natatory setae. Pereiopod 5 consisting of five distinct segments, extending only to base of uropods. Maxilliped 3 and pereiopods 1-5 with a coxal spine plus accessory seta. Edge of hind-body adjacent to insertion of pereiopods 1-4 dorsally with a prominent triangular, posteriorly directed spine. Uropods well developed, relatively short, rounded; outer ramus not much longer than inner, not extending beyond posterior margin of telson in midline. Pleopods elongated; rami slender and widely divergent, with little or no indication of articulation to protopodite; endopod longer than exopod, with incipient appendix interna indicated medially beneath cuticle. Gill buds present.

Coloration of reared phyllosomas. An orange red chromatophore is located in stage I on the eye, at the anterior end of the fore-body on each side between the median eye and the base of the antennule, in each lobe of the lower lip, near the edge of the hind-body on each side between the base of pereiopod 1 and maxilliped 3, and on each side of the fore-body near the lateral border. Two chromatophores are present at the posterior end of the hind-body near the base of the abdomen. Chromatophores are located

on the appendages at the distal end of the basis, carpus and propodus of pereiopods 1-3. A small chromatophore may be visible at the distal end of the third and fourth segments of maxilliped 3, at the end of the fourth segment of maxilliped 2, and on the coxa of pereiopods 1-3 near the base of the coxal spine. Additional chromatophores appear in subsequent stages at various points on the hind-body and on the first five segments of pereiopods 1-4. A chromatophore is present on the outer antennular flagellum and near the base of the antenna. The chromatophore near the edge of the fore-body disappears after stage V or VI.

The Postlarva of *Scyllarus nearctus*
(Figure 37)

Material. Two postlarvae were obtained through metamorphosis in the laboratory of final phyllosomas captured at G-96. One is somewhat imperfectly formed; the other, 16 mm in length, is in fairly good condition. Two other postlarvae, 17 and 18 mm in length, were produced by metamorphosis in the laboratory of phyllosomas collected at P-641. The larger specimen, illustrated in fig. 37, is deposited in the Invertebrate Museum of this Institute (Acc. No. 32.3588). I have examined three additional specimens from the natural environment which are similar to those obtained in the laboratory. Two were captured in midwater in the Straits of Florida; the third was taken in an otter trawl at a depth of 62-69 m south of Dry Tortugas,

Florida, near the type locality of *Scyllarus nearctus*. The collection data are given in Table 10. I have also examined the holotype of *Arctus depressus* (USNM 35392).

Measurements. Measurements of the largest specimen from the natural environment are: TL 19.0; length of carapace in midline 6.8 mm; width of carapace at anterolateral angles 7.8 mm. Corresponding measurements of the smallest specimen are 17.0, 6.0 and 6.7 mm. The illustrated postlarva measures 18.0, 5.9 and 7.0 mm.

Description. The recently metamorphosed postlarvae obtained in the laboratory were more or less transparent except near the lateral borders of the carapace and abdominal segments, at which were distributed numerous golden brown chromatophores. Small, inconspicuous chromatophores were sparsely distributed over the dorsal surface of the carapace and abdominal tergites. Red chromatophores were located on the eye, on the pereiopods, and on the sternum near the base of each pereiopod. A black median eye was visible in the tissue beneath the rostral protuberance. The postlarvae rested on the bottom either in the typical reptant position or on their backs; at no time did I observe them to swim. A description follows.

Exoskeleton relatively rigid. Carapace depressed. Anterolateral angles acute, produced anteriorly. Middorsal ridge of carapace relatively low, with a cardiac and a gastric eminence. Rostral protuberance small, rounded. A denate lateral carina on each side of carapace, interrupted

TABLE 10

LIST OF STATIONS AT WHICH POSTLARVAE OF *SCYLLARUS NEARCTUS* WERE TAKEN

Station	Date (D/M/Y)	Time	Position Lat. N	Position Long. W	Gear	Gear depth(m)	TL (mm)
SL 110 2	29/III/64	1135-1205	$25^{\circ}37'$	$80^{\circ}02'$	3/4m plank. net	40	19.0
G-322	25/V/64	2054-2225	$25^{\circ}41-44.5'$	$79^{\circ}53'$	6' IKMT	110?	17.0
G-565	12/IV/65	1720-1800	$24^{\circ}25-26'$	$82^{\circ}58'$	10' otter trawl	62-69	18.5

behind orbit. Lateral border of carapace with a relatively shallow incision behind eye, followed posteriorly by a second incision and a few obscure notches. Posterior margin of carapace with an acute notch in midline. Proximal (fixed) article of antenna with a prominent, obtuse process projecting anteriorly; a similar smaller process at posteromedial angle of proximal movable article. Lateral border of latter with two fairly prominent teeth; apex acute; a ridge running to apex; medial border dentate. Distal border of terminal antennal article cut into five fairly deep, little separated lobes, outer broadest, inner smallest; a small sixth lobe indicated medially. Sternum behind base of pereiopod 5 terminating in a prominent, posteriorly directed spine. Abdomen about twice length of carapace in midline, tapering posteriorly. Abdominal segments devoid of sculpture. Posterodorsal margin of segments 1-4 with an acute notch in midline, that of segment 4 the shallowest. Segments 2-5 with a slight median carina. Pleura of segments 2-4 terminating in a small but distinct posteriorly directed, spiniform tip. Pleopods in form typical of postlarva; both rami well developed, slender, fringed with plumose setae; endopod with a cylindrical appendix interna provided distally with several minute hooks. Short, nonsetose vestiges of exopods present at distal end of basis of pereiopods 1-4.

Discussion. Bouvier (1915: 290-291) mentioned that he had been able to refer to Scyllarus americanus a postlarva

collected by the BLAKE in the Caribbean, and suggested that the specimen described as *Arctus depressus* by Smith (1881) might be regarded as the second postlarval stage of *S. americanus*. He noted that *Arctus depressus* differed from his specimen chiefly in having a spiniform point on the pleura only of the second abdominal segment. In a subsequent paper (1917: 114-115) Bouvier again discussed these specimens, observing that *Arctus depressus* differed from the Caribbean postlarva principally in the lowness of the gastric and cardiac eminences of the carapace, by the restriction of the pleural points to the second abdominal segment, and by its slightly greater size. He reaffirmed his opinion that *Arctus depressus* was a postlarva of the second stage, but asked "est-il bien celui du *S. americanus*?" Bouvier (1925: 450, pl. 8, fig. 2) provided a more complete description and a figure of the postlarva, 16 mm in length, which he had earlier assigned to *S. americanus*. It was taken at a depth of 80 fathoms off Sand Key, Florida. He again pointed out the differences between the latter and Smith's *Arctus depressus*.

As shown earlier in the present work, neither Bouvier's specimen nor *Arctus depressus* can be considered postlarvae of *Scyllarus americanus*. I find by direct comparison that *Arctus depressus* differs from the postlarvae reported herein principally in the feature noted by Bouvier (1915), namely the absence of a spiniform point at the tip of the pleura of abdominal segments 3 and 4. *Arctus depressus*

does not appear to be damaged, but the small points might easily be broken, or the specimen could be aberrant in this feature. In view of the close similarity in other respects, I feel reasonably confident that both *Arctus depressus* and Bouvier's specimen are postlarvae of *Scyllarus nearctus*. With the possible exception of *S. faxoni*, *S. nearctus* is the only known western Atlantic species of the genus with a final phyllosoma large enough to produce at metamorphosis a postlarva 16 to 19 mm in length. Unfortunately, under the present international rules of nomenclature Smith's name *depressus*, although founded on an immature form, would have priority over *nearctus* for the species.

Bouvier (1917) asked with regard to the possibility that *Arctus depressus* might be the postlarva of *S. americanus*: "Les phyllosomes de cette espece, entraines par les courants, pourraient-ils parfois gagner ces regions?" The occurrence of larvae of *Scyllarus nearctus* off the New England coast can now be documented. Sims (1968) recently reported as *Scyllarides* a phyllosoma 18.9 mm in length, collected on 2 Sept. 1964 in the North Atlantic 400 miles (645 km) east of Cape Cod. Judged from his description, this larva is without doubt the subfinal stage of *Scyllarus nearctus*. A second specimen (5.1 mm in length) assigned to *Scyllarides* by Sims was collected on 8 Sept. 1962, 300 miles (483 km) east of Cape May Light (southern tip of New Jersey). This phyllosoma, which according to Sims is similar to Gurney's (1936: 431, fig. 36) *Scyllarides* sp.,

would correspond to stage V or VI of *Scyllarus nearctus*. The present study indicates that *S. nearctus* has a larval life of three or four months, and Williams (1965) recorded ovigerous females off North Carolina in June. These data coincide with the occurrence of *Arctus depressus* and a subfinal phyllosoma of *S. nearctus* off the New England coast in early September.

Gurney (1936: 430, fig. 35) reported a stage I phyllosoma from Bermuda which appears to be identical in all respects with the stage I phyllosoma of *Scyllarus nearctus*. He designated the specimen *Scyllarides* sp., chiefly because that was the only genus known from Bermuda. Lebour (1950, fig. 3) designated as "*Scyllarides* A" a similar stage I phyllosoma from the plankton around Bermuda. Although to my knowledge no species of *Scyllarus* has ever been taken at Bermuda, the conclusion that adults of *S. nearctus* must occur in that vicinity seems inescapable. The probable occurrence of this species at Bermuda may be associated with the longer duration of larval life compared to that found in the present study for other western Atlantic species of the genus.

Gurney (1936: 427, Table X) listed three phyllosomas of *Scyllarus*, 5.5-18 mm in length, collected by the DISCOVERY in the South Atlantic off the coast of southern Brazil. These larvae probably belong to *S. nearctus*. He illustrated parts of a specimen 13 mm in length (fig. 34, a-c), which appears to correspond to the stage VII described

herein, although it is somewhat larger than the present specimens in a similar stage of development. In the collection of the USNM are a number of phyllosomas similar to those of *S. nearctus*, taken by the U. S. Bureau of Fisheries ALBATROSS Philippine Expedition 1907-1908.

The phyllosomas of *S. nearctus* are more similar to those from the eastern Atlantic and Mediterranean Sea attributed to *Scyllarus arctus* (L.) by Stephensen (1923), Santucci (1925) and Kurian (1956) than to any western Atlantic species. Stephensen and Santucci each recognized nine phyllosoma stages. Gurney (1942) mentioned that a specimen corresponding to Stephensen's stage VII molted to the latter's stage IX. Kurian gave eight stages, but there probably is a stage between his V and VI, and it is not certain that his stage VIII represented the final phyllosoma.

At the time of the investigations cited above, *S. arctus* was considered the only representative of its genus in the Mediterranean. Forest and Holthuis (1960) have since found that a second species of *Scyllarus*, *S. pygmaeus* (Bate), previously known from the eastern Atlantic, "occurs in the Mediterranean, where it is far from rare, but probably has always been mistaken for juvenile *Scyllarus arctus*." It therefore seems likely that the sequences of stages described as *S. arctus* may have included phyllosomas of both that species and *S. pygmaeus*. This would explain certain discrepancies among the three different accounts in size and corresponding degree of morphological development

of the various stages.

As shown in the present study in the sections dealing with *Scyllarides*, the three phyllosomas from the Mediterranean which Stephensen (1923) referred to *Scyllarides latus* cannot be considered larvae of that genus. They belong in all probability either to *Scyllarus arctus* or *Scyllarus pygmaeus*. According to Stephensen these specimens, 4-5 mm in length, corresponded roughly to stage IV of *Scyllarus arctus*, which they closely resembled except for the greater length of the telson spines and the somewhat more advanced development of the antenna and pereiopod 4. Santucci (1925) pointed out that his specimens in the early stages were more advanced morphologically at a corresponding size than those described as *S. arctus* by Stephensen. He mentioned with regard to the telson spines only that in his stage V (6-7.5 mm) they were "molto lunghe." Bate (1888, pl. 12D, fig. 1) reported a phyllosoma 6.5 mm in length from the Cape Verde Islands under the name *Phyllosoma furcicaudatum*, referring to the deeply forked telson. He suggested that it might be the larva of *Ibacus*. Gurney (1936: 431, fig. 36) designated as *Scyllarides* sp. a similar specimen from the vicinity of the Cape Verde Islands. Both of the above phyllosomas are probably slightly later stages belonging to the same species of *Scyllarus* as the larvae referred by Stephensen to *Scyllarides latus*. To clarify the question of specific differences between the phyllosomas of the two Mediterranean species of *Scyllarus*, a comparison of laboratory

reared stages is desirable. The form with the greatly elongated telson spines will probably prove to be the larva of S. pygmaeus.

Gurney (1936: 428, fig. 32) tentatively referred to stage VII of Scyllarus arctus a phyllosoma from the Gulf of Guinea. In view of present knowledge concerning the distribution of the genus Scyllarus in the eastern Atlantic (see Forest, 1963), this specimen probably belongs to either S. paradoxus Miers, S. posteli Forest or S. caparti Holthuis.

C. Scyllarus chacei Holthuis

Materials and methods. An ovigerous female was collected on 20 July 1966 by R/V JOHN ELLIOTT PILLSBURY in the extreme southwestern Caribbean Sea off the coast of Panama (9°30.5-31.0'N, 79°51-52.5'W). The specimen was taken in a 10' otter trawl at a depth of approximately 60 meters. It was placed in a compartment of a plastic tray at a temperature of about 15°C, and on 25 July was transported to Miami by air. After the temperature was allowed to rise gradually to 25°C, the animal was transferred to a 2½-gallon aquarium provided with running sea water at a temperature of 28.5°C. On the night of 29 July most of the embryos were released from the egg capsules in a non-viable condition and died without emerging from the embryonic cuticle. Only a few free-swimming phyllosomas were obtained. These were placed in individual compartments of a plastic tray and reared at 25°C.

On 26 January 1967 an ovigerous female was collected by the Florida State Board of Conservation R/V HERNAN CORTEZ at Hourglass Station D (27°37'N, 83°58'W), in the Gulf of Mexico off St. Petersburg, Florida. The specimen was taken in a 45' trawl at a depth of 55 meters. It was brought to the Florida State Board of Conservation Marine Laboratory at St. Petersburg by Mr. William G. Lyons and

and maintained in a 2½-gallon glass jar provided with aeration. The water was changed about every second day.

A large hatching occurred in the early morning of 11 February. Only stage I phyllosomas were observed. That afternoon a few hundred phyllosomas were pipetted into compartments of plastic trays, which on the following day were transported by automobile to the Institute of Marine Sciences at Miami. The larvae were transferred to individual compartments and reared at various temperatures. Trays of starved individuals were also maintained. Tap water was used to make dilutions for a salinity experiment.

The female is deposited at the Florida State Board of Conservation Marine Laboratory.

Among the collection of phyllosoma larvae dealt with by Robinson and Dimitriou (1963a, b) were about 76 specimens in various stages which I identified as _S_. _chacei_ by comparison with reared material. Several other phyllosomas of this species were collected by Institute of Marine Sciences research vessels in the Atlantic off the north coast of Florida, in the Straits of Florida and in the Caribbean Sea off the coast of Panama. The collection data for all planktonic specimens of _S_. _chacei_ examined are given in Table 11. Representative reared and planktonic stages are deposited in the Invertebrate Museum of this Institute (Acc. No. 32.3597).

Results. Starved larvae failed to molt (fig. 38). Total mortality of 18 individuals at each temperature

TABLE 11

LIST OF STATIONS AT WHICH PHYLLOSOMAS OF SCYLLARUS CHACEI WERE TAKEN

Station	Date (D/M/Y)	Position		Time	Gear	Gear depth(m)	Number of specimens	TL mm
		Lat. N	Long. W					
G-9	25/V/62	25°42'	80°01-09'	2206-2306	IKMT	26-50	1	7.3
G-505	4/II/65	25°39-53'	80°00-01'	1940-2020	2m plank. net	9	1	10.9
G-512	2/III/65	26°07'	79°00'	2018-2036	1m plank. net	sfc	1	10.8
G-764	16/IX/65	25°10'	80°06'	0008-0040	1m plank. net	sfc	1	7.0
P-107	27/VII/64	30°08'	79°23'	2050-2145	1m plank. net	5-15	1	9.9
P-205	12/VIII/64	27°27-28'	79°13-14'	0230-0315	1m plank. net	31	1	3.0
P-326	7/VII/66	9°54'	79°24-26'	2113-2313	10' IKMT	750	1	10.8
P-423	19/VII/66	9°37'	78°44-45'	1906-1921	10' otter trawl	62	1	11.3
P-426	20/VII/66	9°48-50'	79°18'	0136-0238	10' IKMT	20	2	7.5,11.5
TURSIOPS-177	1/VIII/65	26°28-29'	78°45-47'	2214-2303	2m plank. net	45	2	8.7,12.5
1018 G	16/VII/60	25°00'	82°55'	0955	3/4m plank. net	0-47.5	1	4.0
1019 G	"	"	"	0955	"	"	3	4.3-10.5
1021 G	"	"	"	1042	"	"	4	4.3-6.6
1023 G	"	"	"	1042	"	"	2	4.9-10.2
1159 G	5/VIII/60	"	"	1130	"	"	1	7.3
1272 G	1/X/60	"	"	2048	"	"	1	4.6
1274 G	"	"	"	2126	"	"	2	7.1,7.6
1276 G	"	"	"	2128	"	"	3	7.3-8.3
1449 G	8/XII/60	"	"	2327	"	"	1	6.0
1451 G	"	"	"	0038	"	"	2	6.3,7.6
1703 G	20/V/61	"	"	1008	"	"	8	3.0-11.7
1704 G	"	"	"	1043	"	"	4	4.6-10.7
1705 G	"	"	"	1116	"	"	3	4.7-11.4
1760 G	24/VI/61	"	"	0850	"	"	4	4.7-final
1761 G	"	"	"	0851	"	"	2	4.5,7.3
1763 G	"	"	"	0928	"	"	10	4.6-11.6
2785 G	19/IV/62	"	"	1131	"	"	2	7.2,7.3
2786 G	"	"	"	1205	"	"	5	3.2-4.9
2790 G	"	"	"	1545	"	"	1	7.3
1278 AB	2/X/60	24°43'	82°35'	0048	"	0-27.4	2	3.3,7.0
1280 AB	"	"	"	0050	"	"	1	7.4
1282 AB	"	"	"	0130	"	"	1	7.3
1284 AB	"	"	"	0131	"	"	1	7.1
1748 AB	23/VI/61	"	"	1810	"	"	1	6.9
1901 AB	23/VII/61	"	"	1923	"	"	1	1.4
1902 AB	"	"	"	2003	"	"	1	6.4
1903 AB	"	"	"	2004	"	"	1	10.1
2780 J	19/IV/62	24°50'	82°50'	0745	"	0-37.5	1	2.8
2915 J	23/V/62	"	"	1405	"	"	1	3.3
2916 J	"	"	"	1538	"	"	1	10.5
2954 J	6/VI/62	"	"	1348	"	"	2	5.1,11.7
2959 K	"	24°54'	82°32'	1748	"	0-31.1	2	2.0,7.7
2791 U	19/IV/62	25°02'	82°35'	1546	"	0-34.7	1	7.0

occurred within 8 days at 10°, 11 days at 15°, 9 days at 21° and 7 days at 24 ± 1°C. A few individuals at the last temperature eventually molted to stage II after being starved for five days and fed for the first time of the sixth day.

The results of rearing at various temperatures larvae hatched on 11 Feb. 1967 are shown in fig. 39. They were reared in bay water at salinity 33.1 °/oo. At 10°C larvae began dying on the fifth day and total mortality of 18 individuals occurred within 15 days. At 15°C they began dying 11 days after hatching and total mortality of 18 individuals occurred within 26 days. There were no molts at either temperature. At 21°C eight of 18 individuals reached stage IV, and a few survived to stage VI. At 24 ± 1°C slightly more than half of 108 individuals reached stage IV. Mortality was appreciable in subsequent stages; only a few larvae survived to stage VII. Stage VI was first reached 42 days after hatching at 21°C and after 31 days at 24 ± 1°C. At the latter temperature a few individuals out of 36 reared at salinity 26.1 °/oo survived to stage IV.

The duration of the various stages at 24 ± 1°C is given in Table 12. The mean durations of the first four stages were between 5.8 and 6.8 days. That of the next two stages was somewhat greater. Molting was regular at the first ecdysis and became increasingly variable in subsequent stages. The total duration through the first six stages at 24 ± 1°C was about 44 days, based on the values for the mean duration of each stage.

Comparison of reared larvae with specimens from the plankton revealed, as in S. americanus, that growth in the laboratory fell behind that in the natural environment at the ecdysis to stage III. Reared larvae in stage III and subsequent stages were smaller on the average, as well as less developed morphologically, than planktonic specimens in corresponding stages (Table 13). The growth factor for reared larvae declined from 1.45 at the first ecdysis to a little over 1.3 for stages IV-V and V-VI. There was little growth at the ecdysis to stage VII. The growth factor for planktonic larvae remained from 1.4 to over 1.5.

As a rule the degree of morphological development attained by the better developed reared individuals in stages III-V corresponded more or less to that of the least developed larvae from the plankton believed to be in these stages. In the most advanced stage III individuals from the plankton the lateral process of the antenna is indicated, and there are indications of an articulation in the antennular peduncle. In the majority of stage IV specimens maxilliped 1 is present as a low bud, the pleopods are low, distinct buds, the antennal process and uropods are larger than in reared stage IV larvae, and the exopod of pereiopod 4 possesses natatory setae. Of 18 planktonic stage IV individuals examined, the exopod of pereiopod 4 was an elongated rudiment without setae in only three, while in the other 15 specimens the exopod bore any number of natatory setae up to six pairs. The presence of small, incompletely

TABLE 12

DURATION IN DAYS OF THE LARVAL STAGES OF SCYLLARUS CHACEI REARED AT 24 ± 1°C

	I	II	III	IV	V	VI
Mean	6.6	5.8	6.8	6.7	8.2	10.3
Range	6-7	4-7	5-10	5-9	6-13	8-14
No. of larvae	93	80	59	34	23	8

developed gill buds in some reared stage VI individuals suggests that the final phyllosoma would be reached in that stage under more favorable conditions.

An examination and comparison of more than 60 planktonic phyllosomas between stage III and the subfinal stage indicates that most larvae in stage V can be considered subfinal. In many instances the incipient gill buds are indicated beneath the cuticle. The final phyllosoma in nature would therefore in most cases represent stage VI. The smallest, least developed stage V individuals from the plankton, which correspond to the reared stage V, might attain only the subfinal development in stage VI and the final stage in stage VII, as observed for reared larvae. For pusposes of comparison in Table 13, it is assumed that all larvae from the plankton become final phyllosomas in stage VI.

One reared stage VII individual 7.5 mm in length, although a fully developed final phyllosoma, exhibited certain features normally not found in that stage. The distal

TABLE 13

GROWTH OF REARED AND PLANKTONIC LARVAE OF *SCYLLARUS CHACEI*

Stage	Range length (mm)		Mean length (mm)		No. measured		Growth factor	
	reared	planktonic	reared	planktonic	reared	planktonic	reared	planktonic
I	1.35-1.45	--	1.39	1.43	10	1		
II	1.9-2.1	--	2.0	2.0	10	1	1.44	1.40
III	2.6-3.0	2.8-3.4	2.8	3.2	10	8	1.40	1.60
IV	3.4-4.2	4.0-5.6	3.8	4.7	10	18	1.36	1.47
V	4.2-5.4	5.9-8.7	5.0	7.1	9	40	1.32	1.51
VI	5.8-7.4	9.5-12.5	6.6	10.9	12	23	1.32	1.53
VII	6.4-8.8		7.6		10		1.15	

margins of the uropods and telson were fringed with short setae and the appendix interna was indicated as a small protuberance. This specimen was produced by ecdysis of a stage VI phyllosoma in which small gill buds were indicated.

Diagnosis of the Phyllosoma

Stage I 1.35-1.45 mm in length; maxilla 2 usually with four apical setae; medial seta of antennule short; exopod of pereiopod 2 usually with $6\frac{1}{2}$-7 pairs of natatory setae. Fore-body in subsequent stages subquadrate or trapezoidal in outline. Posterolateral telson spines remaining short. Eye and stalk 1.1-1.4 times length of antennule. Length of final stage 9-12 mm. Later stages difficult to distinguish from Scyllarus n. sp.

Characters of the Phyllosoma

The fore-body in stage I is slightly wider than long and nearly twice the width of the hind-body. In subsequent stages the fore-body becomes more or less subquadrate or trapezoidal in outline. It remains slightly wider than long and is 1.6-2.0 times wider than the hind-body, being relatively broader in specimens from the plankton.

The abdomen in early stages is narrow and does not taper much posteriorly. A short spine and three small setae are present at each posterolateral angle. In later stages the abdomen becomes broad at the base, forming a tapering

continuation of the hind-body. In the final stage it is about 3/4 the length of the hind-body and the segments are marked off dorsally near the midline. The spines at the posterolateral angles remain short throughout development, in the final stage extending about to the level of the posterior margin of the telson at the midline.

The eye in stage I is not stalked and is slightly shorter than the antennule. The eye becomes stalked at stage II. In later stages the eye and stalk are 1.1-1.4 times the length of the antennule.

The antennule in stage I has a relatively small seta medially somewhat beyond the middle of its length, and is provided with three terminal aesthetascs plus a short seta at the inner distal angle. The inner flagellum is indicated as a slight protuberance in stage II, is a distinct process in stage III, and in the final stage is about as long as the outer flagellum. In stage IV the outer flagellum is marked off from the peduncular portion, which consists of two segments. In the next stage the antennular peduncle consists of three more or less distinct segments, the lengths of which in the final stage are in the approximate ratio 100:73:57 from proximal to distal.

The antenna in early stages is uniramous and short, with a small seta on each side near the distal end. A small, triangular lateral process appears at stage IV and becomes larger in subsequent stages. The antenna gradually increases in length, but is never as long as the antennule.

In a late stage a division is indicated in the antenna distal to the lateral process. In the final stage the antenna is broad; the medial margin is slightly crenulate distally and bears a few small setae.

Maxilla 1 is biramous, without palp. The coxal endite in stage I is provided with one stout, elongated terminal seta plus one much smaller seta, in addition to one terminal and one subterminal spine or seta. The basal endite bears two strong terminal teeth plus two small subterminal spines or setae and a small seta proximally near the anterior margin. The basal endite acquires a third terminal tooth at stage IV. The second terminal seta of the coxal endite increases in size as development progresses and a few spines or setae are added to each endite.

Maxilla 2 in early stages consists of an elongated basal segment and a small, narrow apical article which usually bears four long, plumose setae. In an occasional specimen only three setae are present. The anterior margin of the basal segment has a small seta distally and one proximally. In most specimens from the plankton the apical segment and terminal setae are lost at the ecdysis to stage IV. In subsequent stages the distal portion, representing the exopod, expands and in the final stage assumes the paddle-shaped form of the scaphognathite.

Maxilliped 1 first appears in well developed stage IV individuals as a low bud posterior to the base of maxilla 2. In subsequent stages it becomes larger and shows indications

of differentiation into an outer lobe. In the final stage maxilliped 1 is a finger-like process with a prominent lobe representing the epipodite on the outer side near the base.

Maxillipeds 2 and 3 each consist of five segments, and lack an exopod. The second segment of maxilliped 3 has a slight bump on the outer side representing the presumptive exopod bud, which shows no differentiation during the course of development. The second segment of maxilliped 2 in the final stage possesses a small, rounded exopod bud.

Pereiopods 1-3 are well developed in stage I. Pereiopod 3 is not much longer than pereiopod 2. The exopod of pereiopod 1 bears 6-7 pairs of natatory setae; that of pereiopod 2 in most individuals possesses $6\frac{1}{2}$-7 pairs of setae. In an occasional specimen only 6 pairs are present. The exopod of pereiopod 3 is a short bud, which becomes an elongated rudiment in stage II and in the next stage acquires 5-6 pairs of natatory setae. Pereiopod 4 is indicated in stage I as a minute bud at the base of the abdomen, and in stage II is an elongated bud up to twice the length of the latter, with the exopod indicated as a minute fold dorsally. In stage III pereiopod 4 is an elongated, more or less distinctly segmented rudiment with a short exopod bud. In the next stage the exopod is elongated, and in many larvae from the plankton may bear up to six pairs of natatory setae. The number of pairs of setae on the exopods increases, but not uniformly, at each ecdysis. The number for various phyllosoma stages is given in Table 14. Pereiopod 5 first

appears in stage II as a minute bud at the base of the abdomen, and at stage IV is an elongated rudiment extending to or slightly beyond the end of the abdomen. In subsequent stages pereiopod 5 becomes divided into five distinct segments. A coxal spine with accessory seta is present on maxilliped 3 and pereiopods 1-3 in stage I, and appears on pereiopods 4 and 5 as they become differentiated. The coxal spines persist throughout larval development. The dactyls at all stages are short and claw-like.

The uropods are first indicated in stage III as low, undifferentiated folds, which become short, bilobed rudiments in stage IV. In subsequent stages the uropods become well developed. In the final stage they are relatively short, oval, and extend to or slightly beyond the posterior end of the telson.

The pleopods are indicated as low folds or buds in stage IV, which in subsequent stages become biramous rudiments. In the final stage they are elongated, with little or no articulation to the protopodite. The endopod is slightly longer than the exopod, with little indication of the appendix interna.

Well developed gill buds are present only in the final stage. Their distribution is as in _Scyllarus americanus_.

Description of Reared Stages

Stage I (fig. 40). Length 1.35-1.45 mm. Fore-body broad, slightly more than 1.1 times wider than long, about

1.9 times wider than hind-body; posterolateral margins covering anterior part of base of maxilliped 3. Abdomen about 1/3 length of hind-body, narrow, tapering slightly posteriorly; a short spine and three small setae at each posterolateral angle. Eye not stalked, slightly shorter than antennule. Latter with a small seta medially somewhat beyond middle of its length, and three terminal aesthetascs plus a short seta at inner distal angle. Antenna uniramous, about 1/3 length of antennule, tapering to point distally; a small seta on each side near distal end. Maxilla 1 biramous, without palp; coxal endite with one stout, elongated terminal seta plus one much smaller seta, and one terminal and one subterminal spine or seta; basal endite with two strong terminal teeth plus two slender subterminal spines or setae; anterior margin with a seta proximally. Maxilla 2 consisting of an elongated basal segment and a small apical article usually bearing four, occasionally three, long plumose setae; anterior margin of basal segment with a small seta distally, another proximally. Maxilliped 1 not indicated. Maxillipeds 2 and 3 each with five segments, without exopod; second segment of maxilliped 3 with a slight bump representing presumptive exopod bud. Pereiopods 1-3 well developed; pereiopod 3 not much longer than pereiopod 2. Exopods of pereiopods 1-2 respectively with 6-7 and usually 6½-7, occasionally 6 pairs of natatory setae; exopod of pereiopod 3 a short bud. Pereiopod 4 indicated as minute bud at base of abdomen. Maxilliped 3 and

pereiopods 1-3 with a coxal spine plus accessory seta.

Stage II (fig. 41). Length 1.9-2.1 mm. Fore-body broadly subquadrate in outline, slightly wider than long, nearly twice width of hind-body. Eye stalked; eye and stalk about 1.2 times length of antennule. Latter with terminal tuft of four aesthetascs plus a small seta at outer distal angle; an additional tuft of two aesthetascs proximal to terminal tuft; inner flagellum indicated as faint protuberance medially with seta at tip. Antenna less than half length antennule. Exopod of pereiopods 1-2 respectively with 7-7½ and 7-8 pairs of natatory setae; exopod of pereiopod 3 an elongated rudiment without setae. Pereiopod 4 an elongated bud up to twice length of abdomen; exopod indicated dorsally as minute fold. Pereiopod 5 a minute bud at base of abdomen.

Stage III (fig. 42). Length 2.6-3.0 mm. Eye and stalk 1.2-1.4 times length of antennule. Outer flagellum of latter with an additional tuft of one or two aesthetascs, not clearly marked off from peduncular portion; inner flagellum a distinct process with seta at tip and smaller subterminal seta. Antenna not quite half length of antennule. Exopod of pereiopods 1-2 respectively with 8-9 and 9 pairs of natatory setae; exopod of pereiopod 3 well developed, with 5-8 pairs of setae. Pereiopod 4 an elongated rudiment several times length of abdomen, consisting of six more or less distinct segments; coxal segment with small spine; exopod a short, nonsetose bud. Pereiopod 5 a bud up to

1/2 length of abdomen. Uropods indicated as low, undifferentiated folds.

Stage IV (fig. 43). Length 3.4-4.2 mm. Fore-body subquadrate in outline, slightly wider than long, 1.9-2.0 times wider than hind-body. Abdomen short, slightly broader at base. Posterior margin of telson more or less straight; posterolateral spines not elongated. Eye and stalk about 1.2 times length of antennule. Antennular peduncle with two distinct segments; proximal twine length of distal; outer flagellum more or less distinctly marked off from peduncular portion. Antenna slightly more than half length of antennule, with small triangular process laterally. Basal endite of maxilla 1 in some specimens with a third, somewhat smaller terminal tooth. Maxilla 2 somewhat shortened; apical segment and setae still present in majority of specimens, absent in the most well developed individuals. Maxilliped 1 not indicated. Exopod of pereiopods 1-3 respectively with 10-11, 11-12 and 8-9 pairs of natatory setae. Pereiopod 4 up to 2/3 length of pereiopod 3; exopod elongated, in the most well developed specimens with two or three pairs of natatory setae. Pereiopod 5 an elongated bud extending about to end of abdomen; coxal segment and small spine beginning to differentiate. Uropods short, distinct buds, in most individuals shallowly bilobed. Pleopods in the most well developed individuals indicated beneath cuticle.

Stage V (fig. 44). Length 4.2-5.4 mm. Fore-body quadrate in outline, slightly wider than long, 1.7-1.8 times

wider than hind-body. Abdomen less than 1/2 length of hind-body, broad at base, tapering posteriorly. Posterior margin of telson convex, more or less rounded. Eye and stalk 1.1-1.2 times length of antennule. Antennular peduncle with indications of a third segment. Antenna nearly 2/3 length of antennule, extending slightly beyond antennular peduncle; triangular outer process larger. Basal endite of maxilla 1 with three subequal terminal teeth. Maxilla 2 in some individuals still with remnants of apical setae; in well developed specimens setae missing and distal portion beginning to expand. Maxilliped 1 a low rounded bud posterior to base of maxilla 2. Exopod of pereiopods 1-3 respectively with 12-13, 12-14 and 10-11½ pairs of natatory setae. Exopod of pereiopod 4 well developed, with 6-8 pairs of natatory setae. Pereiopod 5 slightly longer than abdomen; coxal segment, with short spine, clearly demarcated; remainder of appendage indistinctly segmented. Uropods expanded, biramous rudiments not extending to posterior margin of telson. Pleopods four pairs of distinct buds with trace of bifurcation at tip.

Stage VI (fig. 45). Length 5.8-7.4 mm. Fore-body more or less trapezoidal in outline, broad anteriorly, tapering somewhat posteriorly; slightly wider than long, 1.6-1.7 times wider than hind-body; posterolateral margins covering anterior part of base of pereiopod 1. Abdomen broad, about half length of hind-body, showing some segmentation dorsally at midline. Posterior margin of telson

more or less rounded; posterolateral spines extending slightly beyond level of posterior margin of telson at midline. Eye and stalk 1.1-1.3 times length of antennule. Antennular peduncle with three distinct segments; inner flagellum about 3/4 length of outer flagellum. Antenna shorter than antennule, broader than before; outer process prominent; a division indicated in antenna distal to process. Maxilla 2 with distal portion somewhat expanded. Maxilliped 1 a slightly elongated, conical bud showing signs of differentiation into an outer lobe. Maxillipeds 2 and 3 without exopod buds. Exopod of pereiopods 1-4 respectively with 14-15, 15-16, 12½-14 and 9-11 pairs of natatory setae. Pereiopod 5 longer than abdomen, consisting of five more or less distinct segments. Uropods, oval, extending about to posterior end of telson. Pleopods biramous; rami subequal in length. Small, incompletely developed gill buds present in the most well developed individuals.

Stage VII (fig. 46). Length 6.4-8.8 mm. Fore-body trapezoidal in outline, slightly wider than long, 1.6-1.7 times wider than hind-body; posterolateral margins covering most of base of pereiopod 1. Abdomen roughly 3/4 length of hind-body; segments marked off dorsally near midline; lateral margins of abdomen crenulate due to convexity of side of each segment. Posterior margin of telson more or less straight in middle; posterolateral spines not conspicuous, extending about to level of posterior margin of telson at midline. Eye and stalk about 1.1-1.2 times length

of antennule. Lengths of segments of antennular peduncle in approximate ratio 100:73:57 from proximal to distal. Inner antennular flagellum about as long as outer flagellum; latter with numerous aesthetascs. Antenna broad, slightly shorter than antennule; a division indicated distal to lateral process, another indicated beneath cuticle near base of antenna; medial margin shallowly crenulate distally, with a few small setae. Coxal endite of maxilla 1 with two stout, elongated terminal setae plus smaller terminal and subterminal spines or setae; basal endite with three strong terminal teeth plus a few spines or setae. Maxilla 2 expanded distally in paddle-shaped form of scaphognathite. Maxilliped 1 a relatively short finger-like process with an oval lobe laterally representing epipodite. Second segment of maxilliped 2 with indications of an exopod bud. Maxilliped 3 without distinct exopod bud. Exopod of pereiopods 1-4 respectively with 15-17, 16-18, 14-15½ and 10-12½ pairs of natatory setae. Pereiopod 5 with five segments, extending to or slightly beyond end of telson. All dactyls short and claw-like. Maxilliped 3 and pereiopods 1-5 with a relatively small coxal spine. Uropods well developed, extending to or slightly beyond end of telson; exopod oval, articulated at base, not much longer than endopod. Pleopods slender, elongated; endopod slightly longer than exopod, with incipient appendix interna scarcely indicated. Well developed gill buds present in better developed individuals.

TABLE 14

NUMBER OF PAIRS OF NATATORY SETAE ON THE EXOPODS OF PEREIOPODS 1-4 IN VARIOUS PHYLLOSOMA STAGES OF SCYLLARUS CHACEI

Reared	Stage		P. 1	P. 2	P. 3	P. 4
	I		6-7	6-7	ex. bud	
	II		7-7½	7-8	0	
	III		8-9	9	5-6	ex. bud
	IV		10-11	11-12	8-9	0
	V		12-13	12-14	10-11½	6-8
	VI		14-15	15-16	12½-14	9-11
	VII		15-17	16-18	14-15½	10-12½
Plankton		Length(mm)				
	I	1.43	7	7	ex. bud	
	II	2.0	7	8	0	
	III	2.8	10	10	6½	ex. bud
		3.0	8½	9	5	"
		3.2	9	9½	6	"
		3.4	10	10	6	"
	IV	4.0	11	11	8	0
		4.3	11	11	8½	4½
		4.5	10	11	8	½
		4.6	11	11½	9	1
		4.9	11	12	10	6
		4.9	12	13	10	5
		5.6	13	13	10	5
	V	5.9	13	14	11	8
		6.3	14	14	12	10
		6.6	13	13	11	8
		6.9	14	15	12	9
		7.0	13	14	11	8
		7.3	14	15	13	9
		7.6	16	17	14	11
		7.9	15	16	13	11
		8.7	16	17	14	11
	VI	9.5	15	15	13	11
		10.2	16	16½	14	11
		10.8	17	17	15	12
		11.3	18	18	16	13
		11.5	18	18½	16	13½
		11.6	15	16	14	12
		12.5	18½	18	17	13

Coloration of reared phyllosomas. An orange red chromatophore is located in stage I at the anterior end of the fore-body on each side between the median eye and the base of the antennule, in each lobe of the lower lip, and near the edge of the hind-body on each side between the base of pereiopod 1 and maxilliped 3. Two chromatophores are present at the posterior end of the hind-body near the base of the abdomen. Chromatophores are located on the appendages at the distal end of the basis, carpus and propodus of pereiopods 1-3. In subsequent stages additional chromatophores appear on the eye, at various points on the hind-body, and on the basis, ischiomerus, carpus and propodus of pereiopods 1-4. There may be a small chromatophore near the base of the antenna, at the distal end of the fourth segment of maxilliped 2, and at the end of the third and fourth segments of maxilliped 3.

Discussion. Among the scyllarid phyllosomas in the collection of Robinson and Dimitriou (1963a, b) which I have examined, larvae of S. americanus predominated over those of S. chacei in an approximate ratio of 4:1. Phyllosomas of S. chacei were collected at five stations on the Tortugas Shelf, all within about 50 kilometers north and northeast of Dry Tortugas, over depths ranging from 17 to 26 fathoms.

Records of ovigerous females and the seasonal distribution of the larvae indicate that some spawning of S. chacei may occur throughout most of the year. Phyllosomas

of *S. chacei* were collected on the Tortugas Shelf in April, May, June, July, August, October and December, and in the Straits of Florida in February, March, May, August and September. According to Williams (1965), ovigerous females have been taken off Florida in March, South Carolina in July, Surinam in August and September and northeast Brazil in November. Holthuis (1959) reported ovigerous females (under the name *S. americanus*) off Surinam in July. The specimen from the Gulf of Mexico which produced larvae in the present study was collected in January.

The rearing experiment indicates that complete larval development of *S. chacei* at 25°C would require about six weeks, slightly longer than for *S. americanus*. The difference in duration does not appear to be sufficient to be a significant factor in the much wider geographic distribution of adult *S. chacei* in the western Atlantic.

The Postlarva of *Scyllarus chacei*

Materials and methods. A subsurface haul with a 3/4-meter plankton net was taken in the Florida Current off Miami on 8 March 1968, at about midday. Mr. Robert Bzdyl returned the plankton sample to the laboratory for sorting. A final phyllosoma, identified as *Scyllarus chacei* by comparison with reared material, was removed and placed in a ½-gallon glass jar half-filled with water collected previously in the Florida Current. The jar was placed in a constantly darkened room at a temperature of about 22°C.

Recently hatched brine shrimp nauplii were provided; the phyllosoma was not observed to feed. The water was changed every second or third day. Metamorphosis to the postlarva occurred in the early morning of 16 March. The animal was transferred to a fingerbowl with a layer of sand on the bottom. At no time was the postlarva seen to swim. It died that night and was preserved in 5 per cent formalin. The specimen is deposited in the Invertebrate Museum of this Institute (Acc. No. 32.3598).

Two somewhat larger postlarvae collected in plankton in the Florida Current off Miami correspond in morphology to the one obtained in the laboratory and may belong to S. chacei. One postlarva was taken in the same sample as the above phyllosoma; the other was collected by Dr. Harding B. Owre on 14 July 1967.

Measurements. The final phyllosoma, measured from the exuvium, was approximately 11 mm in length. Measurements of the resulting postlarva are: TL 8.2 mm; length of carapace in midline 3.1 mm; width of carapace at anterolateral angles 3.6 mm; length of abdomen to tip of telson 5.1 mm. Corresponding measurements of the larger of the two postlarvae from the plankton are: 11.2, 3.9, 4.7 and 7.3 mm.

Description. The living postlarva obtained in the laboratory was a pale, translucent brownish yellow, with the exception of the antennae, which were a rather opaque white. There was reddish brown pigment toward the distal end of the outer antennular flagellum. Numerous small, red

chromatophores were present on the pereiopods. A black median eyespot was prominent in the tissue beneath the rostral protuberance. Short, nonsetose vestiges of the larval exopods were present at the outer distal end of the basis of pereiopods 1-4. The pleopods were in the form typical of the postlarval stage, with a well developed, cylindrical appendix interna. A description of this specimen follows.

Carapace depressed; maximum width at anterolateral angles. Latter not projecting much anteriorly. Middorsal ridge of carapace with a cardiac and a gastric eminence; pregastric eminence not present; a small, rounded rostral protuberance. A serrated lateral ridge on each side of carapace, interrupted behind orbit. Lateral border of carapace with a notch behind eye, followed posteriorly by a broader, shallower notch, dentate behind latter. Posterior margin of carapace with a relatively broad, shallow median notch. Proximal article of antennule with a small, triangular tuberole near middle of anterior border. Second article with a rounded anteromedial expansion. Proximal (fixed) antennal article with a triangular, tooth-like projection near middle of anterior border; a smaller tubercle at distomedial angle. First movable article of antenna with lateral border irregularly dentate; a slight ridge running to apex; latter not acute; medial border dentate, with three or four relatively more prominent teeth; distomedial angle with a triangular tubercle. Distal antennal article

of right side with anterior border cut into six relatively shallow, rounded lobes, including small anteromedial lobe; indications of an additional medial lobe. Left antenna with five lobes distally. Sternum behind base of pereiopod 5 not projected in prominent, posteriorly directed spine. Abdominal segments devoid of sculpture. Segments 2-4 with a median carina. Pleura of segment 2 somewhat angular distally; that of segments 3-5 more or less rounded. Segments 1-2 with a relatively shallow median notch at posterodorsal margin; segment 3 with a slight indentation; segment 4 more or less convex, without distinct notch.

Discussion. The postlarva of S. chacei closely resembles that of S. americanus. The differences between adult S. chacei and S. americanus were given by Holthuis (1960) and Williams (1965) as follows: (1) pregastric tooth of carapace bilobed in americanus, broadly rounded anteriorly in chacei; (2) two, seldom three, distinct transverse grooves between posterior marginal groove of carapace and posterior margin in chacei, usually a single groove in americanus; (3) abdominal segments 1-4 with a deep, narrow median incision in posterior margin in americanus, incision very shallow in chacei; (4) abdominal segment 4 with a more or less ridgelike elevation in midline in americanus, no such elevation in chacei.

The first two characters are not evident in the postlarva. I find little consistent difference between postlarvae of the two species in the depth of the median incision

of the abdominal segments. The incisions in most postlarvae of *S. americanus* which I have examined are not as pronounced as they appear in fig. 14. The incision of segment 3 is shallow, and segment 4 shows little or no incision in postlarvae of both species. Abdominal segment 4 in the postlarva of *S. chacei*, as well as in that of *S. americanus*, has an elevated median carina. The median notch at the posterior margin of the carapace seems to be somewhat deeper and narrower in postlarvae of *S. americanus*, but on the whole I find it difficult, from the material at hand, to separate postlarvae of the two species. It is certain that *Arctus depressus* is not a postlarva of *S. chacei*.

D. Scyllarus n. sp.

Materials and methods. Small ovigerous females of a species of Scyllarus were taken by R/V JOHN ELLIOTT PILLSBURY during July 1966 at stations in the extreme southwestern Caribbean Sea off the eastern coast of Panama and the western coast of Colombia. They were collected at depths of 45-64 meters in 10' and 40' otter trawls. The ovigerous females measure 8.0-9.5 mm in carapace length and 21-26 mm in total length. According to Dr. L. B. Holthuis (personal communication), these specimens belong to a new species of Scyllarus, apparently related to S. chacei, which he will describe in the near future.

Several ovigerous specimens were placed in compartments of a plastic tray and were held at 15°C. They were transported to Miami by air on 25 July. The temperature was allowed to rise gradually to 25°C. Some of these specimens were then transferred to a 2½-gallon aquarium provided with running sea water at a temperature of about 28.5°C; others were maintained in compartments of a plastic tray or in fingerbowls.

Small numbers of larvae from different broods were obtained on 29 and 31 July and 2 and 6 August. Hatching in each instance occurred at night. Only stage I phyllosomas were observed. They were placed individually in compartments

of plastic trays and reared in bay or in Florida Current water at 25°C.

The females and representative larval stages are deposited in the Invertebrate Museum of this Institute (Acc. Nos. respectively 32.3589, 32.3599).

Results. The results of the rearing experiment are shown in fig. 50. Survival was rather poor compared to other species of *Scyllarus* reared in the present study. Slightly more than half of 60 individuals reached stage III, but only two survived to stage VI, which was first reached 29 days after hatching.

The duration of the stages is given in Table 15. The mean durations of the first four stages were between 5.2 and 6.2 days. Stage V had a mean duration of 7.5 days, based on two individuals. The duration through the first five stages was about 30 days, based on the values for the mean duration of each stage.

Growth of reared larvae is given in Table 16. The growth factor at the first ecdysis was 1.33. It increased to 1.41 at the next ecdysis, but declined somewhat in subsequent stages to 1.23 at the ecdysis from stage V to Vi.

I found no phyllosomas in the plankton which could be attributed to this species, although there is a possibility that some might have been mistaken for *S. chacei*.

Diagnosis of the Phyllosoma

Stage I 1.23-1.33 mm in length; maxilla 2 with three,

TABLE 15

DURATION IN DAYS OF THE LARVAL STAGES OF *SCYLLARUS* N. SP. REARED AT 25°C

	I	II	III	IV	V
Mean	5.4	5.2	5.4	6.2	7.5
Range	5-7	4-8	4-9	5-8	7-8
No. of larvae	43	36	20	12	2

TABLE 16

GROWTH OF LARVAE OF *SCYLLARUS* N. SP. REARED AT 25°C

Stage	Range length mm	Mean length mm	Number measured	Growth factor
I	1.23-1.33	1.28	10	
II	1.5-1.8	1.7	6	1.33
III	2.3-2.5	2.4	4	1.41
IV	2.8-3.6	3.2	7	1.33
V	3.6-4.5	4.0	10	1.25
VI	4.4-5.4	4.9	7	1.23

four, or occasionally five apical setae; medial seta of antennule short; exopod of pereiopod 2 with six pairs of natatory setae. Fore-body in subsequent stages becoming subquadrate or trapezoidal in outline. Posterolateral telson spines remaining short. Eye and stalk 1.4-1.6 times length of antennule. Later stages difficult to distinguish from *Scyllarus chacei*.

Characters of the Phyllosoma

The fore-body in stage I is slightly wider than long and about 1.7 times wider than the hind-body. In subsequent stages the fore-body becomes more or less subquadrate or trapezoidal in outline, as long as or slightly longer than wide, and 1.6-1.7 times wider than the hind-body.

The abdomen in early stages is narrow and relatively parallel-sided. A short spine and three small setae are present at each posterolateral angle. In later stages the abdomen becomes broad at the base, forming a tapering continuation of the hind-body. The spines at the posterolateral angles remain short throughout development.

The eye in stage I is not stalked and is nearly as long as the antennule. The eye becomes stalked at stage II. At stage IV the eye and stalk are 1.4-1.5 times the length of the antennule, and in subsequent stages they are 1.5-1.6 times longer than the latter.

The antennule in stage I has a relatively short seta medially somewhat beyond the middle of its length, and is provided with three terminal aesthetascs plus a small spine or seta at the inner distal angle. The inner flagellum is indicated as a faint protuberance in stage II, and is a distinct process in stage III. The antennular peduncle is distinctly two-segmented in stage IV. The outer flagellum is clearly marked off from the latter in stage V. In stage VI the antennular peduncle consists of three more or less distinct segments.

The antenna in early stages is uniramous and short, with a small seta on each side near the distal end. A lateral process is indicated as a slight protuberance in stage IV, and appears as a small but distinct triangular process in stage V. The antenna gradually increases in length but is never as long as the antennule.

Maxilla 1 is biramous, without palp. The coxal endite in stage I has one stout, elongated terminal seta plus a much smaller seta in addition to one terminal and one subterminal spine or seta. The basal endite is provided with two strong terminal teeth plus two smaller subterminal spines or setae and a seta proximally near the anterior margin. The basal endite acquires a third terminal tooth in stage V. The second terminal seta of the coxal endite increases in size as development progresses and a few spines or setae are added to each endite.

Maxilla 2 in early stages consists of an elongated basal segment and a small, narrow apical article which may bear three, four, or occasionally five long, plumose setae. The anterior margin of the basal segment has a small seta proximally and one distally. The apical article and setae are lost at the ecdysis to stage V or VI, and in subsequent stages the distal portion, representing the exopod, expands.

Maxilliped 1 first appears in stage V as a low bud posterior to the base of maxilla 2, and becomes larger in subsequent stages. Maxillipeds 2 and 3 each consist of five segments, and lack an exopod.

Pereiopods 1-3 are well developed in stage I. Pereiopod 3 is not much longer than pereiopod 2. The exopod of pereiopod 1 bears usually 6, occasionally 5½, pairs of natatory setae; that of pereiopod 2 has 6 pairs of setae. The exopod of pereiopod 3 is a short bud, which becomes an elongated rudiment in stage II and in the next stage acquires 3½-4½ pairs of natatory setae. Pereiopod 4 is indicated in stage I as a minute bud at the base of the abdomen and in stage II is nearly as long as or slightly longer than the latter, with the exopod indicated as a minute fold dorsally. In stage III pereiopod 4 is an elongated, more or less distinctly segmented rudiment with a short exopod bud. The exopod in stage IV is an elongated, nonsetose rudiment, which in the next stage in most individuals acquires 4-5 pairs of natatory setae. The number of pairs of setae on the exopods increases, but not uniformly, at each ecdysis. Pereiopod 5 is indicated in stage III as a small but at the base of the abdomen, and at stage V is a rudiment extending nearly to the end of the latter. In subsequent stages pereiopod 5 becomes divided into five segments and extends to or slightly beyond the end of the telson. A coxal spine plus accessory seta is present on maxilliped 3 and pereiopods 1-3 in stage I and appears on pereiopods 4 and 5 as they become differentiated. The coxal spines persist throughout development. The dactyls at all stages are short and claw-like.

The uropods are faintly indicated in stage III as folds

in the cuticle and appear in stage IV as small undifferentiated lobes, which are larger and biramous in stage V. In subsequent stages they become well developed, oval in outline, and extend to or slightly beyond the end of the telson.

The pleopods are indicated as low folds in stage V, which in subsequent stages become biramous rudiments.

Small, incompletely developed gill buds are indicated in the most advanced reared stage VI specimen.

Description of Stages

Stage I (fig. 51). Length 1.23-1.33 mm. Fore-body slightly broader than long, about 1.7 times wider than hind-body. Abdomen narrow, about 1/3 length of hind-body, not tapering much posteriorly; a short spine and three small setae at each posterolateral angle. Eye not stalked, approximately equal in length to antennule. Latter with three terminal aesthetascs plus a small spine or seta at inner distal angle; a relatively short seta medially somewhat beyond middle of its length. Antenna uniramous, about 1/3 length of antennule; a small seta on each side near distal end. Maxilla 1 biramous, without palp; coxal endite with one stout, elongated terminal seta plus a much smaller seta and one terminal and one subterminal spine or seta; basal endite with two strong terminal teeth plus two smaller subterminal spines or setae and a seta proximally near anterior margin. Maxilla 2 consisting of an elongated basal segment and a small apical article bearing three, four, or

occasionally five long, plumose setae; anterior margin of basal segment with a small seta proximally and one distally. Maxilliped 1 not indicated. Maxillipeds 2 and 3 each with five segments, without exopod. Pereiopods 1-3 well developed; pereiopod 3 not much longer than pereiopod 2. Dactyls short, claw-like. Pereiopod 4 indicated as minute bud at base of abdomen. Exopod of pereiopod 1 usually with 6, occasionally $5\frac{1}{2}$, pairs of natatory setae; exopod of pereiopod 2 with 6 pairs. Exopod of pereiopod 3 a short bud. Maxilliped 3 and pereiopods 1-3 with a relatively short coxal spine plus accessory seta at its base.

Stage II (fig. 52). Length 1.5-1.8 mm. Fore-body as long as or slightly longer than wide, nearly 1.7 times wider than hind-body. Eye stalked; eye and stalk about 1.2 times length of antennule. Latter with a tuft of two aesthetascs proximal to terminal tuft; latter consisting of four aesthetascs plus a seta at outer distal angle; inner flagellum beginning to differentiate as faint protuberance with seta at tip. Antenna slightly more than 1/3 length of antennule. Exopod of pereiopods 1-2 respectively with 6-7 and $6\frac{1}{2}$-7 pairs of natatory setae. Exopod of pereiopod 3 an elongated rudiment without setae. Pereiopod 4 a rudiment nearly as long as or slightly longer than abdomen; exopod indicated as minute fold dorsally. Pereiopod 5 not clearly indicated.

Stage III (fig. 53). Length 2.3-2.5 mm. Fore-body slightly longer than wide, 1.7-1.8 times wider than hind-body. Abdomen not much broader at base. Eye and stalk

1.3-1.4 times length of antennule. Antennular peduncle not distinctly segmented; inner flagellum a short cylindrical process; outer flagellum not marked off from peduncular portion, with an additional tuft of two aesthetascs. Antenna less than 1/2 length of antennule. Exopod of pereiopods 1-2 respectively with 7-8 and 8 pairs of natatory setae. Exopod of pereiopod 3 functional, with $3\frac{1}{2}$-$4\frac{1}{2}$ pairs of natatory setae. Pereiopod 4 a rudiment several times length of abdomen, consisting of six more or less distinct segments; coxal segment with rudiment of spine; exopod a short, non-setose bud. Pereiopod 5 a bid at base of abdomen. Uropods faintly indicated as folds in cuticle.

Stage IV (fig. 54). Length 2.8-3.6 mm. Fore-body about 1.1 times longer than wide, 1.7 times wider than hind-body. Abdomen short, not much broader at base. Eye and stalk 1.4-1.5 times length of antennule. Antennular peduncle with two more or less distinct segments; outer flagellum not clearly marked off from peduncular portion. Antenna about 1/2 length of antennule; incipient outer process indicated as slight protuberance. Basal endite of maxilla 1 with two terminal teeth. Maxilla 2 still with apical segment and plumose setae. Maxilliped 1 not indicated. Exopods of pereiopods 1-3 respectively with 8-10, 9-11 and 6-8 pairs of natatory setae. Exopod of pereiopod 4 an elongated rudiment without setae. Pereiopod 5 a short bud less than 1/2 length of abdomen. Maxilliped 3 and pereiopods 1-4 with a coxal spine. Uropods small, undifferentiated lobes. Pleopods

not indicated.

Stage V (fig. 55). Length 3.6-4.5 mm. Fore-body more or less subquadrate in outline, slightly longer than wide, 1.6-1.7 times wider than hind-body. Abdomen nearly 1/3 length of hind-body, becoming broader at base. Postero-lateral telson spines relatively short. Eye and stalk 1.5-1.6 times length of antennule. Antennular peduncle with two distinct segments, in some specimens with indications of a third; outer flagellum clearly demarcated from peduncle. Antenna more than half length of antennule, with small, distinct lateral process. Basal endite of maxilla 1 in most specimens with a third, somewhat smaller terminal tooth; coxal endite with two stout terminal setae nearly equal in length, plus a few smaller spines or setae. Maxilla 2 somewhat shortened; apical article and setae still present in some individuals. Maxilliped 1 indicated as low bud posterior to base of maxilla 2. Exopod of pereiopods 1-3 respectively with 10-11½, 11-12 and 8½-10 pairs of natatory setae. Exopod of pereiopod 4 functional, with 1-5, in most specimens 4-5, pairs of setae. Pereiopod 5 a rudiment somewhat shorter than abdomen; coxal segment partially differentiated, with small obtuse rudiment of spine. Uropods small, shallowly cleft buds. Pleopods faintly indicated as folds in cuticle.

Stage VI (fig. 56). Length 4.4-5.4 mm. Fore-body becoming trapezoidal in outline, about as long as wide, 1.6-1.7 times wider than hind-body. Eye and stalk 1.5-1.6

times length of antennule. Antennular peduncle with three more or less distinct segments. Antenna extending about to end of antennular peduncle; lateral process larger. Basal endite of maxilla 1 with three subequal terminal teeth. Maxilla 2 shortened, with or without apical article and setae; not much expanded distally. Maxilliped 1 a short conical bud. Exopod of pereiopods 1-4 respectively with 11-12, 12-13, 10-11 and 6-8½ pairs of natatory setae. Pereiopod 5 a rudiment extending slightly beyond end of telson; coxal segment clearly demarcated, with spine; remainder of appendage indistinctly divided. Uropods biramous rudiments extending nearly to end of telson. Pleopods four pairs of distinct, undifferentiated buds.

Coloration of phyllosomas. An orange red chromatophore is located in stage I at the anterior end of the fore-body on each side between the median eye and the base of the antennule, in each lobe of the lower lip, and near the edge of the hind-body on each side between the bases of pereiopod 1 and maxilliped 3. Two chromatophores are present on the eye and in the midline of the hind-body near the base of the abdomen. Chromatophores are located on the appendages near the distal end of the basis, carpus and propodus of pereiopods 1-2, and at the distal end of the carpus and propodus of pereiopod 3. In subsequent stages additional chromatophores appear on the hind-body and on the ischiomerus, carpus and propodus of pereiopods 1-4. A small chromatophore may appear near the base of maxilla 1 and at the distal

end of the fourth segment of maxilliped 2.

Discussion. The most well developed specimen obtained (stage VI) is slightly more advanced in morphology than the one described above; the pleopods are shallowly bilobed and small, poorly developed gill buds are present. Despite the indication of gill buds in this larva, it does not appear that the final phyllosoma would be attained before stage VII, at least under laboratory conditions. The average morphological advances at the ecdyses from stage III through VI were somewhat less marked than those observed in the development of *S. americanus* and *S. chacei*. In view of the decrease in the growth factor, there is a possibility that the development of *Scyllarus* n. sp. may have been slightly retarded.

Since the total duration through stage V was about 30 days, the length of larval life is probably comparable to that of *S. chacei*. The morphological similarity of the larvae to those of *S. chacei* confirms the close relationship of the two species.

E. Scyllarides aequinoctialis (Lund)

Materials and methods. An ovigerous female approximately 240 mm in total length was taken on 14 March 1964, in a lobster trap on the outer reef off Tavernier in the Florida Keys. The animal was brought to the laboratory and held in a 15-gallon aquarium provided with running sea water. Hatching occurred on the night of 7 April. A second ovigerous female 250 mm in length was collected on 10 April 1967, in a lobster trap on the reef off Marathon, Florida. This specimen was held in a similar way. Hatching occurred on the night of 12 May. Water temperature in the aquaria to the dates of hatching varied from 22 to 26°C. Recently deposited eggs were bright orange and measured 0.60-0.68 mm in diameter. Just prior to hatching they were approximately 0.80 mm. I did not estimate the number of eggs, but it appeared to be comparable to that of Panulirus. The female collected in 1967 is deposited in the Invertebrate Museum of this Institute (Acc. No. 32.3590).

In both instances the larvae emerged from the egg in the form of the so-called naupliosoma, swimming actively at or near the surface by means of the setose antenna. Within a few minutes most of the naupliosomas underwent an ecdysis and appeared as stage I phyllosomas. These were reared at

various temperatures.

I have examined about 80 phyllosomas from the plankton which apparently belong to this species, not including several in the collection of the USNM (59586). The collection data are given in Table 17. Most were taken in the Atlantic off the coast of Florida and between the northern Bahama Islands and Bermuda. Thirty-six individuals of mean length 11.4 mm were collected at P-164, at which several other scyllarid phyllosomas as well as over 2,000 phyllosomas of Panulirus were taken during a one-hour tow with a 2-meter plankton net. A specimen 22 mm in length was collected at P-454 in the extreme southern Caribbean Sea off Pt. Gallinas, Colombia. Representative reared and planktonic stages are deposited in the Invertebrate Museum of this Institute (Acc. No. 32.3591).

Through the courtesy of the staff of the Florida State Board of Conservation Marine Laboratory I had the opportunity to examine the large specimens described as "Phyllosome A," "Phyllosome B," and "Phyllosome C" by Sims (1964), and later reported by Sims (1965a) as stages 11 and 12 of Parribacus sp.

Results. In no instance did starved larvae molt. Their survival at various temperatures is shown in fig. 60. The mean survival time in days for 18 individuals at each temperature was 14.3 at 10°C, 16.7 at 15°C, 20.4 at 20°C and 15.8 at 24 ± 1°C. Although a few individuals survived for up to 34 days at 10°C, all larvae at that temperature were

TABLE 17

LIST OF STATIONS AT WHICH PHYLLOSOMAS OF SCYLLARIDES AEQUINOCTIALIS WERE TAKEN

		Position						
Station	(D/M/Y)	Lat. N	Long. W	Time	Gear	Gear depth(m)	Number of specimens	TL mm
G-46	21/VIII/62	25°39.5-50'	79°56-58'	1515-1852	6' IKMT	87	2	14.2,15.4
G-47	21/VIII/62	25°39'	79°40'	1906-1935	6' IKMT	sfc-162	1	11.0
G-98	9/V/63	25°21-24.2'	79°50-51'	1840-2045	6' IKMT	42-48	1	28.8
G-99	9/V/63	25°18-21'	79°50'	2105-2313	6' IKMT	52	1	14.0
G-143	22/VI/63	24°28-31'	80°06-12'	2250-2320	otter trawl?	805	1	26.8
G-331	26/VI/64	25°26-36'	79°41-44.5'	1952-2100	6' IKMT	256	1	21.5
G-337	22/VII/64	26°02'	79°48'	1348-1546	6' IKMT	39	1	4.6
G-343	24/VII/64	25°52'-26°05'	79°20'	1350-1548	6' IKMT	51	6	2.60-14.4
G-344	24/VII/64	26°01-05'	79°20'	1604-1802	6' IKMT	137	1	9.9
G-350	25/VII/64	25°48-52'	79°24-31'	1640-1838	6' IKMT	146	1	final
P-100	26/VII/64	30°06'	78°42'	2000-2100	1m plank. net	3-5	1	11.7
P-107	27/VII/64	30°08'	79°23'	2050-2145	1m plank. net	5-15	1	7.0
P-113	28/VII/64	31°49'	77°51'	1835-1944	10' IKMT	50	1	22.3
P-144	3/VIII/64	32°46'	64°33'	2025-2115	1m plank. net	10	5	2.72-2.96
P-164	7/VIII/64	28°27-30'	73°39-42'	2115-2215	2m plank net	2	36	6.1-22.8
P-165	7/VIII/64	28°25-27'	73°42'	2235-2335	1m plank net	20-60	10	9.5-20.0
P-169	8/VIII/64	27°30'	76°27'	2115-2205	1m plank. net	sfc	4	8.0-13.0
P-190	10/VIII/64	27°25'	78°08'	2049-2225	2m plank. net	0-9	1	13.0
P-195	11/VIII/64	27°28'	78°19'	0345-0435	1m plank. net	20	3	9.0-24.8
P-196	11/VIII/64	27°37'	78°27'	0450-0545	1m plank. net	27	4	7.3-12.5
P-454	27/VII/66	12°55-56.5'	72°00-04'	1200-1400	10' IKMT	1500	1	22.0
SL 41 A2	17/X/55	25°35'	79°30'	1535	3/4m plank. net	119	1	13.3
TURSIOPS-167	30/VII/65	26°42'	78°57'	2115-2155	2m plank. net	subsfc	1	13.3
DDS-369	27/V/62	3 mi. off West End, Bahamas		--	1m plank. net	sfc	1	2.55

extremely feeble after seven days, and those which survived longer than two weeks showed only the faintest indications of life.

The results of rearing at various temperatures larvae hatched in 1967 are shown in fig. 61. At 10°C they gegan dying on the fourth day and total mortality of 18 individuals occurred within eight days. There were no molts. At 15°C total mortality of 18 individuals occurred within 18 days, without ecdysis; mean survival was 7.8 days. At 20°C 15 of 36 larvae molted to stage II after a mean duration of 16.1 days in stage I. Only one individual survived to stage III. At 24 ± 1°C more than half of 108 larvae reached stage V, about 25 per cent reached stage VIII, and two individuals survived to a tenth stage. Stage VIII was first reached 72 days after hatching. The intermolt period was considerably shortened at 30°C, but mortality was high; of 54 individuals, none survived beyond stage III.

The duration of the various stages at 20°, 24 ± 1°, and 30°C is given in Table 18. Molting was regular at the first ecdysis, but more variable in subsequent stages. At 24 ± 1°C the mean duration was 8.1 days for stage I, within 11 ± 1 days for the next four stages, and nearly two weeks for stages VI-IX. The duration of stage I at 20°C was about twice that at 24 ± 1°C, and more than three times the duration at 30°C. The total duration through the first eight stages at 24 ± 1°C was 94 days, based on the values for the mean duration of each stage.

TABLE 18

DURATION IN DAYS OF THE EARLY LARVAL STAGES OF *SCYLLARIDES AEQUINOCTIALIS* REARED AT VARIOUS TEMPERATURES

	20°C			24 ± 1°C			30°C		
Stage	Range	Mean	No. of larvae	Range	Mean	No. of larvae	Range	Mean	No. of larvae
I	15-18	16.1	15	8-9	8.1	92	4-6	4.9	12
II	23	23	1	9-15	10.2	84	5-6	5.3	6
III	--	--	--	9-17	11.1	79	---	---	--
IV				8-15	10.7	68			
V				9-18	11.9	50			
VI				11-21	13.8	36			
VII				11-19	13.7	29			
VIII				10-17	14.4	11			
IX				13-14	13.3	3			

Growth of reared larvae is given in Table 19. The growth factor was 1.26 at the first ecdysis and 1.28 at the second, but decreased in subsequent stages to only 1.08 at the molt from stage VIII to IX. A steady progression in morphological development was observed among the better developed individuals of each stage through the first eight stages. Specimens in stages IX and X were no more advanced morphologically than the most well developed stage VIII larvae. The latter measure about 6 mm in length. Their development corresponds more or less to that of planktonic phyllosomas at a length of 7-8 mm, in which pereiopod 5 is an elongated rudiment 2-5 times the length of the abdomen and possesses a nonsetose exopod bud.

Stage II phyllosomas from the plankton which may belong to S. aequinoctialis agree with reared stage II individuals in development, but are slightly larger. Two specimens in stage II collected in the Straits of Florida measure 2.55 and 2.60 mm in length, compared to a mean of 2.42 mm for reared larvae. In would appear, therefore, that even at the first ecdysis the growth of larvae in the laboratory is slightly less than in nature. Five stage II phyllosomas taken at P-144 near Bermuda are larger, measuring 2.72 to 2.96 mm in length, but may belong to a different species. If the mean length of planktonic stage II is taken as 2.57 mm, based on the two larvae from the Straits of Florida and assuming that the length of stage I corresponds to laboratory hatched individuals, the growth factor at the first

TABLE 19

GROWTH OF EARLY LARVAL STAGES OF *SCYLLARIDES AEQUINOCTIALIS* REARED IN THE LABORATORY

Stage	No. measured	Mean length (mm)	Growth factor
I	8	1.92	
II	8	2.42	1.26
III	8	3.11	1.28
IV	8	3.59	1.15
V	9	4.13	1.15
VI	8	4.65	1.13
VII	8	5.11	1.10
VIII	12	5.68	1.11
IX	8	6.15	1.08

ecdysis in nature would be 1.34, compared to 1.26 obtained in the laboratory. The growth factor of subsequent stages in the natural environment may decrease, but probably not to the extent observed for reared larvae. Specimens from the plankton which correspond in morphological development to reared stage VIII individuals may represent only the sixth or seventh stage.

The development attained by the most advanced larvae reared appears to be sufficient to permit a positive identification of planktonic larvae of S. aequinoctialis by comparison with reared material. Among specimens from the plankton having a pear-shaped fore-body and pereiopod 5 at the above-mentioned stage of development, I can recognize three similar but different forms, the definitive characteristics of which are just beginning to become evident. One of these, referred to Parribacus in the present study, differs significantly from reared larvae of S. aequinoctialis in the structure of the antenna, and there are slight differences in the shape and proportions of the hind-body. The other form, tentatively referred herein to Arctides, has an antenna similar to S. aequinoctialis but the proportions of the fore- and hind-body are slightly different and the length of the eyestalk relative to that of the antennule is distinctly greater.

The phyllosoma 28.8 mm in length apparently represents the stage of development immediately preceding the subfinal stage and is the largest intact larva of S. aequinoctialis

in the present collection. A single final phyllosoma of this form was taken at G-350 in the Straits of Florida west of Bimini. The anterior portion of the fore-body is damaged, but the rest of the specimen is in good condition.

What are in all probability the last two stages in the development of this species have been described and illustrated by Sims, first in 1964 and later in 1965, from planktonic material collected in the Yucatan and Florida Straits. The subfinal stage (length 33.4 mm) was designated "Phyllosome C" by Sims (1964: 262, fig. 3). One final phyllosoma 36.0 mm in length was designated "Phyllosome A;" another 41.2 mm in length was designated "Phyllosome B." In his 1965 account Sims included these stages in the larval sequence which he attributed to Parribacus sp., designating the larva of 33.4 mm stage 11 (fig. 11) and the final phyllosoma (41.2 mm) stage 12 (fig. 12). Reproductions of the latter figures are given in fig. 77 of the present work. These phyllosomas have a well developed pereiopod 5 with a setose exopod and definitely are not of the same species as the earlier stages in Sims' (1965a) sequence in which pereiopod 5 is rudimentary. They form a continuation of the sequence of stages described herein. The phyllosomas with the rudimentary pereiopod 5 are shown in the present study to belong with probability to Scyllarides nodifer rather than to Parribacus.

Available data concerning the occurrence of ovigerous females and the seasonal distribution of the various

phyllosoma stages are insufficient to permit an accurate estimate of the duration of larval life of S. aequinoctialis. Complete larval development would undoubtedly require several months, since larvae after three months in the laboratory were still in a relatively early stage of morphology. The large number of relatively small individuals taken at P-164 in August may reflect a spring spawning on the reefs of the Bahamas and Florida Keys. Both final phyllosomas reported by Sims were collected in December, but the specimen from G-350 was taken in July. A postlarva in the museum of this Institute (Acc. No. 32.894), possibly belonging to S. aequinoctialis (see Pfeffer, 1881; Bouvier, 1913), was collected at Key Largo in January, 1953 by Dr. G. L. Voss. If spawning is restricted primarily to the spring months (March-May), a larval life of eight or nine months might be indicated. The distributional picture is complicated by the probable transport of larvae from the Caribbean through the Yucatan and Florida Straits (see Sims and Ingle, 1967).

Diagnosis of the Phyllosoma

Stage I 1.9 mm in length, with biramous antenna, pear-shaped fore-body, pereiopod 3 1.3 times length of pereiopod 2, excluding dactyl; exopod of pereiopods 1-2 with 6 pairs of natatory setae. Early stages similar to other species of Scyllarides and related genera. Pereiopod 5 becoming well developed at relatively early stage, with setose exopod by TL 9-10 mm. Phyllosoma identifiable by TL 6-7 mm,

with fore-body slightly wider than hind-body, eyestalk/antennule ratio 1.2-1.4, inner ramus of antenna with articulation, outer ramus a short triangular process. Antenna with remnant of exopod up to TL 21-22 mm; lateral process appearing on second article by TL 22 mm. Fore-body becoming progressively broader anteriorly and increasingly wider than hind-body, in later stages subelliptical in outline. Length of final stage 36-41 mm.

Characters of the Phyllosoma

The fore-body in stage I is pear-shaped, about 1.1 times longer than wide and 1.4 times wider than the hind-body. In early stages the fore-body becomes elongated and its width relative to the hind-body decreases; by stage VI it is only about 1.1 times wider than the latter. In intermediate stages the relative width of the fore-body increases and it becomes progressively broader anteriorly. In late stages the fore-body is subelliptical in outline, about 1.3 times longer than wide and 1.3 times wider than the hind-body.

The abdomen in stage I is narrow, rectangular, and about 1/2 the length of the hind-body. A short spine and three small setae are present at each posterolateral angle. These become inconspicuous in subsequent stages and soon disappear entirely. A posterior concavity in which the abdomen is situated forms in the hind-body as the rudiment of pereiopod 5 moves away from the base of the abdomen. After

TL about 11 mm the latter no longer extends to the level of the base of pereiopod 5 until a late stage. The abdominal segments are first marked off dorsally near the midline. In the final stage the posterolateral margin of segment 5 is drawn out posteriorly on each side as a short obtuse process. The posteroventral margin on each side of segments 2-5 is produced into a small, ventrally directed tubercle. The posterodorsal margin at the midline of segments 4 and 5 is produced into a spiniform process, that of segment 4 being the larger. These correspond to similar processes in the postlarva of Scyllarides spp. The telson is without spines.

The eye in stage I is not stalked and is 1.2-1.3 times longer than the antennule. The eye is stalked in stage II and in subsequent stages the stalk increases in length. At TL 6-7 mm the eyestalk is 1.2-1.4 times the length of the antennule, and at TL 9-11 mm the ratio is 1.5-1.6. This ratio increases to a maximum of nearly 1.8 in a late stage and decreases in the last stages to roughly 1.5.

The antennule in stage I is unsegmented. It bears three terminal aesthetascs plus a small seta at the inner distal angle and a minute toothlike seta at the outer distal angle. A small seta is present on the medial side slightly beyond the middle of its length. The inner flagellum is indicated as a small bud in stage IV. By stage VII the outer flagellum is clearly marked off from the peduncular portion and the latter consists of two segments.

Between TL 11-13 mm a third segment forms in the antennular peduncle. In the final stage the segments are subequal in length. The inner flagellum is shorter than the outer. Aesthetascs are added to the latter as development progresses.

The antenna in stage I is somewhat shorter than the antennule and stouter than the latter. It divides into two branches at a point beyond the middle of its length. The rami are not articulated, but the basal portion of the endopod is articulated with a slightly longer, cylindrical apical segment which bears four small setae at or near the distal end. The exopod is stouter and slightly longer than the endopod and terminates in two short spines. In early stages the antenna decreases in relative size, and the outer ramus is reduced to a small triangular process. By TL about 20 mm the exopod is represented only by a small toothlike projection at the outer distal end of the basal antennal segment, and it soon disappears entirely. Between TL 11-13 mm an articulation forms between the basal portion of the antenna bearing the reduced outer ramus and the base of the endopod. At the same time there are indications of an additional articulation in the latter. In following stages the antenna increases gradually in length and becomes divided into five more or less distinct segments, including the basal portion. At TL about 22 mm the lateral process of the antenna becomes differentiated as a small triangular projection at the outer distal end of the second article. It increases in size in subsequent stages and in the final

stage is much expanded. In the final stage the antenna is slightly longer than the antennule. Both margins of the terminal article, representing the flagellum, as well as those of the lateral process, are entire.

Maxilla 1 in stage I is biramous and without a palp, although the anterior margin of the basal endite is elevated proximally and bears a fairly long, slender seta. The latter becomes smaller in subsequent stages. The basal endite terminates in two strong terminal teeth and bears two slender subterminal spines, one near the anterior and one near the posterior margin. The coxal endite has one stout, elongated terminal seta plus a smaller seta and a subterminal spine. The basal endite acquires a third terminal tooth at stage V. Later in development a third terminal seta is added to the coxal endite. Smaller spines or setae are added to both endites as development progresses.

Maxilla 2 in stage I consists of an elongated basal segment and a small, narrow apical article bearing four long, plumose setae. The anterior margin of the basal segment has two small setae distally and one proximally. The long apical setae begin to disappear at TL about 8 mm, and by TL 9 mm most individuals are without setae and the division between the basal portion and the narrow apical portion is no longer distinct. The distal portion, representing the exopod, begins to expand at TL about 24 mm; in the final stage it assumes the paddle-shaped form of the scaphognathite.

Maxilliped 1 is first indicated at TL 12-13 mm as a slight elevation posterior to the base of maxilla 2. In subsequent stages it becomes a short conical bud, which in late stages shows indications of differentiation. In the final stage maxilliped 1 is a finger-like process with an oval lobe laterally representing the epipodite.

In early and intermediate stages maxillipeds 2 and 3 each consist of five segments and lack an exopod, although the second segment of maxilliped 3 has on its outer side a slight bump representing the presumptive exopod bud. At TL 28 mm the latter appears as a small oval bud, which in the final stage is a short, slender rudiment without setae. Late in development a swelling representing the incipient exopod bud appears on the second segment of maxilliped 2. At TL 28 mm it is a small rounded protuberance, which in the final stage is a short, oval bud. A lobe representing the epipodite is attached at the outer distal end of the coxal segment of maxilliped 2 in the final stage.

Pereiopods 1 and 2 in stage I have well developed exopods bearing six pairs of long, plumose natatory setae. I found no variation in the number of setae among specimens examined from two different broods. Pereiopod 3 in stage I is well developed, measuring about 5.5 mm in length (excluding the dactyl), or about 1.3 times the length of pereiopod 2. The latter is slightly longer than pereiopod 1. The exopod of pereiopod 3 in stage I is only a short, rudimentary bud, which acquires setae in stage III. The dactyls

of pereiopods 1-3 in stage I are relatively short and claw-like. At about the fifth stage the dactyl of pereiopod 3 begins to increase in relative length and in subsequent stages it becomes markedly elongated and blade-like, whereas the dactyl of pereiopods 1-2 remains short and claw-like throughout development. The distal portion of the propodus of pereiopods 1-2 acquires numerous spines or setae.

Pereiopod 4 is represented in stage I by a minute bud at the base of the abdomen, which in the immediately following stages becomes fully differentiated, with an exopod. The latter may acquire a few setae in stage V. Pereiopod 4 soon becomes, like pereiopod 3, longer and more robust than pereiopods 1-2. The dactyl, which is initially short, assumes a blade-like form similar to that of pereiopod 3, although it is always somewhat less than half the length of the latter.

Pereiopod 5 is indicated as a minute bud at the base of the abdomen in stage III. By stage VI it has become a somewhat elongated bud extending about to the middle of the abdomen and is a short distance removed from the base of the latter. At this point it is evident that pereiopod 5 is destined to become well developed at a relatively early stage. In the next stage the rudiment of pereiopod 5 extends about to the end of the abdomen and the exopod is indicated as a minute fold dorsally near the tip. In the following stage the pereiopod becomes an elongated rudiment several times the length of the abdomen. The coxal segment

is clearly demarcated and the remainder of the appendage shows incomplete differentiation. The exopod is a somewhat elongated bud. Between TL 8-9 mm pereiopod 5 consists of six more or less distinct segments and may extend nearly to the distal end of the basis of pereiopod 4. The exopod is elongated, and at TL about 9 mm it acquires natatory setae. In subsequent stages pereiopod 5 becomes as fully developed as pereiopods 3 and 4. The propodus is quite long; the dactyl is short. The lengths of the various segments of the pereiopods in the first and final phyllosoma stages are given in Table 20. The number of pairs of natatory setae on the exopods of pereiopods 1-2 increases by one per molt in the first few stages, but later more than one pair may be added at an ecdysis. The number of pairs of setae on the exopods in various stages is given in Table 21.

A prominent coxal spine with an accessory seta at the base is present on pereiopods 1-3 in stage I. The coxa of maxilliped 3 has a small seta but no spine. In subsequent stages the coxal spines become less conspicuous and they disappear entirely at TL about 10-11 mm. No coxal spines are present in later stages.

The uropods are first indicated at TL about 12 mm as slight swellings, which soon become low folds in the cuticle. At TL 16 mm they appear as small undifferentiated lobes. At TL 21 mm the uropods are short buds shallowly cleft at the tip, which by TL 25 mm are oval, biramous rudiments, with the outer ramus longer than the inner and extending

nearly to the posterior end of the telson. In the last stages the uropods are well developed, extending beyond the end of the telson; the outer ramus is articulated at the base.

The pleopods first become evident at TL about 20 mm as four pairs of low folds in the cuticle, which at TL 23 mm are distinct, rounded buds. By TL 27 mm the pleopods are shallowly cleft at the tip, and at TL 29 mm they are biramous, with the rami subequal in length. In the final stage the pleopods are elongated and leaf-like. The rami are subequal in length and show indications of articulation to the protopodite. The endopod has on its medial side a short, free cylindrical process representing the appendix interna.

Gill buds are present only in the final stage. Their distribution is given in Table 22. Sims (1964, 1965a) stated that bilobed gills are present on segment one of pereiopods 1-5, with an additional set of three gills on the dorsal hind-body at the origin of pereiopods 1-4. I find only a pleurobranch at pereiopod 5, as in other final phyllosomas, located dorsally on the hind-body. According to Calman (1909), the last thoracic somite in decapods "is invariably destitute of mastigobranchia, podobranchia, or arthrobranchiae, though it may carry a pleurobranchia and a setobranchia." I also find only one pleurobranch dorsally on the thorax at the origin of pereiopod 1, in addition to an arthrobranch and the bilobed bud, representing podobranch plus epipodite, on the coxa.

TABLE 20

LENGTH IN MM OF THE VARIOUS SEGMENTS OF THE PEREIOPODS IN THE FIRST AND FINAL PHYLLOSOMA STAGES OF *SCYLLARIDES AEQUINOCTIALIS*

Stage I	coxa	basis	ischiomerus	carpus	propodus	dactyl
Pereiopod 1	0.27	0.68	0.70	0.46	1.43	0.37
" 2	0.27	0.68	0.90	0.58	1.75	0.48
" 3	0.27	0.60	1.62	0.72	2.36	0.32
Final stage						
Pereiopod 1	2.8	10.0	4.5	4.2	13.1	1.5
" 2	3.0	9.2	5.9	5.6	16.5	2.0
" 3	3.2	8.6	11.7	10.0	23.5	7.3
" 4	3.2	11.5	11.5	10.7	26.0	3.6
" 5	3.1	13.0	11.2	10.2	27.4	2.1

Pereiopods 1-4 of final stage from G-350; pereiopod 5 from Sims' "Phyllosome B"

TABLE 21

NUMBER OF PAIRS OF NATATORY SETAE ON THE EXOPODS OF PEREIOPODS 1-5 IN VARIOUS PHYLLOSOMA STAGES OF SCYLLARIDES AEQUINOCTIALIS

Reared Stage	P. 1	P. 2	P. 3	P. 4	P. 5
I	6	6	ex.bud		
II	7	7	ex.rud.		
III	8	8	3-5	ex.bud	
IV	9	9	5-7	ex.rud.	
V	10-11	10-11	7-9	0-3	
VI	11-12	11-12	8½-10	4-6	
VII	11-12	11-12	9½-11½	6-8½	ex.ind.
VIII	12-13	12-13	11-12	8-9½	ex.rud.
IX	12-14	12-14	11-13	8½-10½	ex.rud.
X	14	15	13½	11½	ex.rud.
Planktonic TL (mm)					
5.9	12	12	9½	5½	ex.ind.
7.1	13	13	11	8	ex.rud.
7.7	13	14	12½	10	ex.rud.
8.5	14	15	13	11	ex.rud.
8.8	15	15	14	12	0
8.9	15	16	14	12½	5½
9.0	16	16	14	13	5
10.4	16	16	15	14	7
11.9	18	18	17	15½	9
12.3	19	19	18	16	11
14.2	19	20	18½	17	13
15.4	20	20	20	19	15
16.2	21	21½	20½	20	17
20.8	24	25	23	23	20
22.8	25	26	25	24	22
26.8	27	28	26	26	25
28.8	27	28	27	26½	24½
"Ph. C" 33.4	28	29	28	28	--
"Ph. A" 36.0	30	30	29	28½	28
G-350 final	30	31	31	30	28
"Ph. B" 41.2	31	31	30½	30	29

TABLE 22

DISTRIBUTION OF GILL BUDS IN THE FINAL PHYLLOSOMA OF *SCYLLARIDES AEQUINOCTIALIS*

		Podobranch	Arthrobranch	Pleurobranch	Epipodite
Maxilliped	2	0	0	0	1
"	3	1	1	1	1
Pereiopod	1	1	1	1	1
"	2	1	1	2	1
"	3	1	1	2	1
"	4	1	1	2	1
"	5	0	0	1	0

The Naupliosoma Stage

(Figure 62)

Description. Fore-body rounded in outline, wider than hind-body. Eye well developed, not stalked, in many specimens folded against fore-body. Median eye present. Antennule uniramous, unsegmented, folded posteroventrally over fore-body. Antenna stout, biramous, projecting posterolaterally; endopod without distinct articulation, terminating in one stout, tapering seta fringed with a single series of setules; endopod of phyllosoma stage, with articulation, clearly visible beneath cuticle of proximal portion. Posterior margin of exopod bearing seven stout, tapering setae including terminal seta considerably smaller than others, fringed on each side with setules. Labrum, lobes of lower lip and mandibles well developed. Maxilla 1 bilobed. Maxilla 2 an elongated bud without setae. Maxilliped 1 not present. Maxillipeds 2 and 3 each consisting of five segments, without exopod. Pereiopods 1-3 well developed, segmented, curled anteriorly over thorax; exopods of pereiopods 1-2 without natatory setae; exopod of pereiopod 3 a small bud. Abdomen well developed, rectangular. Appendages without external spines or setae.

Discussion. A free-swimming prephyllosoma stage of Jasus Ialandii was observed by Gilchrist (1913). He called attention to the superficial resemblance of the larva at this stage to a nauplius, while pointing out that "the larva is much more advanced in organization than a nauplius,

this latter stage having presumably been passed through much earlier in the development of the egg." He stated that "for convenience the larva may be called a naupliosoma or described as being in a naupliosoma stage." In a subsequent paper Gilchrist (1916) emphasized that the name "was not intended to suggest any direct relation to the nauplius stage, and, in so far as it does so, is inappropriate." A different view was held by Gurney (1942), who felt that the stage represented by the embryonic cuticle among decapods in general is "properly to be regarded as a modified Nauplius."

The naupliosoma of Jasus appears to resemble closely that of Scyllarides aequinoctialis. In Jasus the endopod of the antenna terminates in two stout setae, whereas in S. aequinoctialis it bears only one seta. In the naupliosoma of both species the exopod of the antenna is provided with a total of seven setae, including the small terminal seta. The duration of this stage in Jasus as observed by Gilchrist was 4-6 hours. Archey (1916) also described the naupliosoma of Jasus and mentioned that it "could not be found after an hour or more." In both hatchings of S. aequinoctialis, most naupliosomas that were observed individually molted to the phyllosoma stage within a few minutes; the precise moment of hatching was not determined. My observations of S. aequinoctialis agree with Gilchrist (1916), who found that the naupliosoma stage of Jasus "moves toward the light and undergoes ecdysis without descending from the surface of

the sea." Naupliosomas of S. aequinoctialis swimming at the surface in a small fingerbowl were observed under the microscope to molt and emerge as stage I phyllosomas.

Harada (1958) reported free-swimming naupliosoma larvae of Ibacus ciliatus (von Siebold) that within thirty minutes molted and took the form of the phyllosoma. Comparison of the stage I phyllosoma described by Harada with the figures given for the first phyllosoma of two species of Ibacus by Dotsu, Seno and Inoue (1966) indicates that Harada was dealing with I. novemdentatus Gibbes. As in S. aequinoctialis, the endopod of the antenna of the naupliosoma of this species of Ibacus terminates in a single plumose seta, and the exopod bears a total of seven. Harada mentioned that "larvae of the form of the naupliosoma hatched out when the eggs in the advanced stage of Scyllarides squamosus (H. Milne Edwards) were artificially shaken in the laboratory," but they were unable to swim.

Sheard (1949) stated with reference to Panulirus longipes (Milne-Edwards) (= P. cygnus George) that "The first stage is a naupliosoma quickly followed by the first of a number of phyllosoma stages," and further that "The naupliosoma avoids light, creeping into rock cracks etc. for protection." George and Cawthorn (1962), however, reported that larvae of this species "hatched directly," presumably in the first phyllosoma stage, from a berried female in an aquarium. In a subsequent paper George (1962) called attention to certain differences between newly hatched

larvae of P. cygnus and older stage I phyllosomas, but regarded "as early phyllosoma stage I" the recently hatched specimens presumably referred to by Sheard as naupliosomas. George stated, "The 'naupliosoma' is not here regarded as a distinct stage separated by a moult."

C. von Bonde (1936) observed an earlier stage in Jasus lalandii immediately after leaving the egg which he termed the "prenaupliosoma." He reported that the prenaupliosoma stage was relatively quiet for a short time after hatching, but that it soon "appeared very lively" and after about eight hours assumed "the shape of the naupliosoma accompanied by an ecdysis." Feliciano (1956) described a non-swimming prenaupliosoma stage in the embryonic development of Panulirus argus. The significance of prephyllosoma stages has been discussed by Sims (1965b), who reported prenaupliosoma larvae presumably of P. argus from the plankton. As Sims stated, the question "is whether the nauplio-somal stages are a normal part of the free life development of the spiny lobster or whether they are the result of premature rupture of the egg."

In my opinion Sims' suggestion that hatching in a prenaupliosoma or naupliosoma stage "is the norm for certain species" is correct. A free-swimming prephyllosoma stage which subsequently molted to the stage I phyllosoma is documented for Jasus, Ibacus and now Scyllarides. In these genera the antenna of the prephyllosoma stage is biramous and specially adapted for swimming, being stout and provided

with plumose setae. It is possible that this stage has escaped detection in certain other species due to its short duration and the fact that hatching often occurs at night. Gilchrist (1913) suggested that the significance of the naupliosoma stage is "that it enables the young to ascend more rapidly, and with certainty, to the surface than in the case with the slowly moving phyllosoma, which is more adapted to a horizontal mode of progression."

In other genera such as Scyllarus and Panulirus emergence of the stage I phyllosoma from the embryonic cuticle appears to be associated with the process of normal eclosion, and in these a prephyllosoma stage is probably the result of premature rupture of the egg. Gurney (1942) stated that in those decapods which hatch at a zoea stage the embryonic cuticle "is commonly moulted in the act of hatching," but that "in many cases, especially among Brachyura, it is retained for a short time after hatching, and the larvae may swim actively." A stage similar to the so-called prenaupliosoma can be produced by osmotic or mechanical rupture of late eggs of any species of scyllaridean lobster. It has not been demonstrated, however, that such stages are capable of molting into free-swimming phyllosomas (see Sims, 1965b), nor that certain genera normally hatch in any form other than the stage I phyllosoma. It is not clear why a free-swimming prephyllosoma stage should be found in some genera of Scyllaridea but not in others.

Description of Reared Phyllosoma Stages

Stage I (fig. 63). Length 1.87-1.94 mm. Fore-body pear-shaped, 1.1-1.2 times longer than wide, 1.4 times wider than hind-body. Abdomen narrow, rectangular, about half length of hind-body; a short spine and three small setae at each posterolateral angle. Eye not stalked, 1.2-1.3 times length of antennule. Antennule unsegmented, with three terminal aesthetascs plus a small seta at inner distal angle and a minute toothlike seta at outer distal angle; a small seta medially somewhat beyond middle of its length. Antenna somewhat shorter, but stouter than, antennule; divided into two branches at point beyond middle of its length; exopod slightly longer than and not articulated with endopod, terminating in two short spines; endopod consisting of basal portion articulated with cylindrical terminal segment, latter with three or four small terminal setae. Maxilla 1 biramous, without palp; basal endite with two strong terminal teeth plus two slender subterminal spines, one near anterior and one near posterior margin; anterior margin proximally with elevation bearing a slender seta; coxal endite with one stout, elongated terminal seta plus a shorter, more slender seta and a spine. Maxilla 2 consisting of a basal segment and a smaller, narrow apical article bearing four long plumose setae; anterior margin of basal segment with two small setae distally and one proximally. Maxilliped 1 not indicated. Maxillipeds 2 and 3 each with five segments, without exopod; second segment of maxilliped 3

with small bump laterally representing presumptive exopod bud. Pereiopods 1 and 2 well developed, with setose exopod bearing six pairs of long, plumose natatory setae. Pereiopod 3 well developed, about 1.3 times length of pereiopod 2, excluding dactyl; exopod a short rudimentary bud. Dactyl of pereiopods 1-3 relatively short and claw-like. Pereiopods 1-3 with coxal spine plus accessory seta at base; maxilliped 3 with small seta without spine. Pereiopod 4 a minute bud at base of abdomen. Pereiopod 5 not indicated.

Stage II (fig. 64). Length 2.3-2.5 mm. Fore-body pear-shaped, 1.3-1.4 times longer than wide, 1.2-1.3 times wider than hind-body. Eye stalked; eyestalk about 0.6 times length of antennule. Antennule with four terminal aesthetascs. Antenna shorter than antennule; outer ramus with a single terminal spine. Maxillae and maxillipeds as before. Exopods of pereiopods 1 and 2 each with 7 pairs of swimming setae. Exopod of pereiopod 3 an elongated rudiment without setae. Pereiopod 4 a bud up to 1/2 length of abdomen; exopod indicated as minute fold dorsally. Pereiopod 5 not indicated.

Stage III (fig. 65). Length 2.8-3.4 mm. Fore-body pear-shaped, 1.4-1.6 times longer than wide, 1.2-1.3 times wider than hind-body. Eyestalk 0.7-0.8 times length of antennule. Antennule 1.6-1.7 times longer than antenna, with an additional aesthetasc proximal to terminal tuft. Outer ramus of antenna slightly longer than inner, tapering to point distally. Exopods of pereiopods 1 and 2 each with 8

pairs of swimming setae. Pereiopod 3 with functional exopod bearing 3-5 pairs of swimming setae. Pereiopod 4 an elongated rudiment 1-3 times length of abdomen, with indistinct segmentation; exopod indicated dorsally as minute bud. Pereiopod 5 a minute bud at base of abdomen.

Stage IV (fig. 66). Length 3.2-4.0 mm. Fore-body pear-shaped, 1.6 times longer than wide, 1.2-1.3 times wider than hind-body. Eyestalk 0.8-0.9 times length of antennule. Inner flagellum of antennule indicated as minute protuberance on medial side with short seta at tip. Outer ramus of antenna approximately equal in length to inner. Exopods of pereiopods 1-3 respectively with 9, 9 and 5-7 pairs of swimming setae. Pereiopod 4 an elongated rudiment consisting of six more or less distinct segments; exopod a nonsetose bud. Pereiopod 5 a small bud at base of adbomen.

Stage V (fig. 67). Length 3.8-4.5 mm. Fore-body pear-shaped, about 1.6 times longer than wide, 1.2-1.3 times wider than hind-body. Length of eyestalk approximately equal to that of antennule. Antenna about 1/2 length of antennule; outer ramus as long as or slightly shorter than inner ramus. Basal endite of maxilla 1 in some individuals with a third terminal tooth. Dactyl of pereiopod 3 somewhat elongated. Exopod of pereiopod 4 an elongated rudiment without natatory setae, or, in well developed specimens, with up to three pairs of setae. Pereiopod 5 a relatively small bud near base of abdomen.

Stage VI (fig. 68). Length 4.2-5.0 mm. Fore-body

pear-shaped, 1.7-1.8 times longer than wide, about 1.1 times wider than hind-body. Length of eyestalk equal to or slightly greater than that of antennule. Antenna slightly less than 1/2 length of antennule; inner ramus slightly longer than outer ramus. Basal endite of maxilla 1 with three subequal terminal teeth. Dactyl of pereiopod 3 distinctly elongated, nearly twice length of dactyl of pereiopod 2. Pereiopod 4 well developed but shorter than other pereiopods; dactyl short; exopod functional, with 4-6 pairs of swimming setae. Pereiopod 5 a bud a short distance removed from base of abdomen and up to 1/2 length of latter.

Stage VII (fig. 69). Length 4.8-5.8 mm. Fore-body pear-shaped, 1.6-1.8 times longer than wide, 1.1-1.2 times wider than hind-body. Eyestalk up to 1.1 times length of antennule. Outer flagellum of antennule more or less distinctly marked off from peduncular portion; latter divided into two segments by a more or less distinct articulation; inner flagellum a short conical bud. Antenna about 1/3 length of antennule. Pereiopod 5 an elongated bud extending to or slightly beyond end of abdomen; exopod indicated dorsally as minute fold near tip.

Stage VIII (fig. 70). Length 5.0-6.4 mm. Fore-body pear-shaped, 1.6-1.8 times longer than wide, 1.05-1.10 times wider than hind-body. Latter with shallow posterior concavity in which abdomen is situated. Abdomen narrow, rectangular, about 1/4 length of hind-body; spine and setae at posterolateral angles much reduced or absent. Eyestalk

1.1-1.2 times length of antennule. Antennular peduncle with two segments. Antenna about 1/3 length of antennule; outer ramus short, pointed, in most specimens not extending beyond articulation in inner ramus. Basal endite of maxilla 1 with three strong terminal teeth plus a few smaller spines or setae; coxal endite with two stout, elongated terminal setae plus a few terminal and subterminal spines or setae. Maxilla 2 in most specimens still with four long, plumose apical setae. Maxilliped 1 not indicated. Maxillipeds 2 and 3 essentially unchanged except for addition of a few spines or setae. Pereiopod 3 considerably longer than pereiopods 1 and 2; pereiopod 4 slender, somewhat longer than pereiopods 1 and 2. Dactyl of pereiopods 1 and 2 short, claw-like; dactyl of pereiopod 3 elongated, blade-like, nearly three times length that of pereiopod 2. Dactyl of pereiopod 4 short. Pereiopods 1-3 with a small coxal spine. Pereiopod 5 in less developed individuals as in previous stage. In well developed specimens, pereiopod 5 an elongated rudiment up to four times length of abdomen, with coxal segment more or less clearly demarcated; remainder of appendage with indistinct segmentation; exopod a somewhat elongated bud without setae.

Coloration of reared larvae. The phyllosomas are pigmented with bright orange-red to red bands, each of which appears to be formed by several irregular chromatophores in an expanded state. In early stages the only chromatophores on the body are located in each lobe of the lower lip and

at the base of the abdomen. In later stages a small chromatophore may appear at the anterior end of the fore-body on each side between the base of the antennule and the median eye. In stage I and in subsequent stages pereiopod 1 has chromatophores only at the distal end of the propodus. Pereiopod 2 has chromatophores at the distal end of the propodus and at the distal end of the carpus. In the first two stages pereiopod 3 also has chromatophores at the distal end of the carpus and propodus. In stage III pigment appears at the distal end of the basis of pereiopod 3 near the attachment of the exopod. Chromatophores first appear on pereiopod 4 in stage IV at the distal end of the propodus. In stage V they are also present at the distal end of the carpus, and in subsequent stages at the distal end of the basis. The pigment at the distal end of the carpus of pereiopods 2-4 may extend across the articulation onto the proximal end of the propodus.

Description of Illustrated Stages from Plankton

Length 8.3 mm (fig. 71). P-164. Fore-body pear-shaped, 1.6 times longer than wide, 1.1 times wider than hind-body. Posterolateral margins of fore-body not quite or just covering anterior part of base of maxilliped 3. Hind-body with shallow posterior concavity in which abdomen is situated; latter narrow, without spines, uropods or pleopods, extending beyond level of base of pereiopod 5. Eye-stalk 1.4 times length of antennule. Antennular peduncle

with two segments; proximal twice length of distal. Antenna short, biramous, rami not articulated, but basal portion of endopod articulated with short cylindrical apical segment; exopod pointed, extending to articulation in endopod. Maxilla 1 biramous, without palp; coxal endite with two stout, elongated terminal setae plus a few smaller terminal and subterminal spines or setae; basal endite with three strong terminal teeth plus a few spines or setae. Maxilla 2 with basal portion not distinctly marked off from narrow apical portion; latter with three long, plumose setae. Maxilliped 1 not indicated. Maxilliped 2 with five segments, without exopod. Maxilliped 3 with five segments; second with slight bump on outer side near middle of its length representing presumptive exopod bud. Pereiopods 1-4 well developed, with setose exopods. Pereiopod 5 an elongated rudiment consisting of six more or less distinct segments, extending nearly to end of basis of pereiopod 4; exopod a slender, elongated rudiment without setae. Pereiopod 1-3 with short coxal spine.

Length 8.9 mm (fig. 72). P-164. Eyestalk 1.5 times length of antennule. Antennular peduncle with two segments. Antenna as before, except outer ramus shorter. Apical portion of maxilla 2 without terminal setae. Maxilliped 1 not indicated. Pereiopod 5 slender, shorter than pereiopods 1-4; exopod with 5½ pairs of natatory setae. Pereiopods 1-3 with small, inconspicuous coxal spine.

Length 13.3 mm (fig. 73). TURSIOPS-167. Fore-body

broader anteriorly, nearly 1.5 times longer than wide, 1.2 times wider than hind-body. Abdomen not extending quite to level of base of pereiopod 5. Eyestalk more than 1.6 times length of antennule. Antennular peduncle with three segments. Antenna extending beyond end of proximal article of antennular peduncle, with three segments: a basal article bearing reduced exopod as obtuse, triangular process at outer distal end; a middle segment showing indications of an additional articulation; and a shorter, cylindrical terminal article. Coxal endite of maxilla 1 with two stout, elongated terminal setae plus a third smaller seta. Maxilla 2 narrow and rounded distally. Maxilliped 1 indicated as slight elevation posterior to base of maxilla 2. Pereiopods without coxal spines. Pereiopod 5 well developed. Uropods indicated as folds in cuticle. Pleopods not indicated.

Length 16.2 mm (fig. 74). P-164. Fore-body nearly 1.4 times longer than wide, 1.2 times wider than hind-body. Abdomen little developed. Telson rounded, without spines. Eyestalk 1.7-1.8 times length of antennule. Antenna not extending to end of second article of antennular peduncle; exopod much reduced. Maxilliped 1 a low bud. Uropods small undifferentiated buds. Pleopods not indicated.

Length 22.8 mm (fig. 75). P-164. Fore-body 1.3 times longer than wide, 1.2 times wider than hind-body, becoming progressively broader anteriorly, narrowing more abruptly at anterior end; maximum width near middle of length. Eyestalk nearly 1.8 times length of antennule.

Antenna not extending to end of antennular peduncle, partially divided into five segments, including basal portion; latter with minute, toothlike projection representing vestige of exopod at outer distal end; second article with small process beginning to differentiate laterally. Distal portion of maxilla 2 beginning to expand, not yet as broad as basal portion. Maxilliped 1 a short conical bud. Incipient exopod of maxilliped 2 indicated as slight swelling on outer side of second segment. Uropods small bilobed rudiments. Pleopods indicated as four pairs of low, undifferentiated buds.

Length 28.8 mm (fig. 76). G-98. Fore-body subelliptical in outline, becoming narrower rather abruptly at anterior end, 1.3 times longer than wide, 1.3 times wider than hind-body. Abdomen extending beyond level of base of pereiopod 5; segmentation indicated dorsally near midline. Posterior margin of telson rounded. Eyestalk nearly 1.6 times length of antennule. Antenna extending to about middle of outer antennular flagellum, with five segments indicated, the second with a prominent triangular process laterally. Distal portion of maxilla 2 broader than basal portion. Maxilliped 1 a bud showing indications of differentiation. Second segment of maxilliped 2 with minute protuberance representing exopod bud. Maxilliped 3 with small, oval exopod bud. Pereiopods 1 and 2 with short, claw-like dactyl. Pereiopod 4 longer, more robust; dactyl longer, blade-like. Uropods biramous, oval; outer ramus longer than inner,

extending beyond posterior end of telson. Pleopods biramous, short; appendix interna not indicated.

Discussion. Our limited knowledge of the larval development of Scyllarides has been derived primarily from phyllosomas taken in the plankton. Verrill (1922) suggested that the form from the West Indies described by Bate (1888) "may belong to Scyllarus or one of the species of Scyllarides, but its origin is very uncertain." Stephensen (1923) apparently was the first to assign phyllosomas to Scyllarides. He tentatively identified as Scyllarides latus (Latr.) three specimens in an early stage from the Mediterranean Sea. Several stage I phyllosomas from the Mediterranean in the vicinity of Messina were regarded by Santucci (1925) as belonging to Scyllarides latus. In a subsequent paper Santucci (1928) described the first phyllosoma of this species from specimens which had been found attached to the pleopods of a female, and confirmed his earlier identification of the planktonic material from Messina. A phyllosoma 3.7 mm in length from the Red Sea was believed by Santucci (1930) to be the third stage in the larval development of S. latus. W. von Bonde (1930) described a sequence of phyllosoma stages from the south and east coast of South Africa, presuming them to be larvae of Scyllarides elisabethae (Ortm.). The results of the investigations cited above were reviewed by Gurney (1936), who referred nine specimens from the eastern Atlantic to Scyllarides, and illustrated a stage I phyllosoma from Bermuda which he thought probably belonged

to this genus. Gurney attempted to recognize the diagnostic characters of the phyllosomas of Scyllarides, and wrote:

> It is probably safe to accept long telson spines in the early stages, and pointed uropods in later ones, as distinctive for the genus; but the length of the antenna does not seem to be a reliable character, and in intermediate stages, when the rudimentary uropods are rounded, the two genera /Scyllarus and Scyllarides/ may be indistinguishable.

Gurney (1942) thought that the larvae characteristic of Scyllarus and Scyllarides "are known with certainty or probability." This is open to question, since planktonic larvae can seldom be identified with certainty. Most subsequent workers, however, followed Gurney's diagnosis for the larvae of Scyllarides. Lebour (1950) designated a stage I phyllosoma from the plankton around Bermuda "Scyllarides A;" a different stage I phyllosoma from the same area was designated "Scyllarides B." Prasad and Tampi (1960) described as Scyllarides sp. a phyllosoma from the west coast of India. In a report on the association of scyllarid phyllosomas with jelly-fish, Shojima (1963) published a photograph of a larva from Japanese waters designated Scyllarides sp. Baisre (1966) gave the relative length of the telson spines for separating phyllosomas of Scyllarides from Parribacus in a key to the stage I phyllosomas of the Scyllaridae. Saisho (1966b) reported phyllosomas from the Indian Ocean similar to the Scyllarides sp. of Gurney and Prasad and Tampi. Sims (1968) has recently assigned to Scyllarides two phyllosomas collected in the North Atlantic

off the eastern coast of the United States.

Unless there is a profound separation among species of the genus, for which I am aware of no evidence, it is clear from the results of the present investigation that virtually all larvae previously attributed to Scyllarides have been misidentified. Stephensen (1923) did not provide a full description of the larvae which he referred to Scyllarides latus, but mentioned that they closely resembled the corresponding stage of Scyllarus arctus. He illustrated (p. 76, fig. 25) only the abdomen and proximal portion of pereiopod 4. Stephensen gave the basis for his identification as follows:

> Owing to the very long apical spines on the tail, this larva can hardly be identical with that of Scyllarus arctus, but since it is at any rate closely allied to this, and as no other species of the group of Phyllosomes laticaudatae but Scyllarus arctus and Scyllarides latus have ever been found in the Mediterranean, it must belong to the latter species.

As mentioned previously, Forest and Holthuis (1960) have since reported the occurrence of Scyllarus pygmaeus (Bate) in the Mediterranean. Stephensen's specimens belong in all probability to one or the other Mediterranean species of Scyllarus. As shown in the present work in the section on Scyllarides nodifer, the phyllosoma from the Mediterranean attributed by Stephensen to Thenus is probably the larva of Scyllarides latus.

Gurney (1936) correctly pointed out that one cannot accept Santucci's (1930, figs. 1-4) specimen of 3.7 mm from

the Red Sea as a larva of Scyllarides, "or even as a Scyllarid at all." The possession of a setose exopod on maxilliped 3 excludes it from the Scyllaridae and places it in the Palinuridae. This larva appears to me to be an early stage of the same species as the peculiar palinurid phyllosoma 9.5 mm in length reported from Perim in the Red Sea by Santucci (1927, pl. 1, fig. 5). He believed the latter to be a larva of Panulirus, the only palinurid genus known from that locality at the time. Belloc (1959) proposed the name Phyllamphion Santucii for this specimen and suggested that it might be the larval form of the genus Puer (= Puerulus), a suggestion made also by Sims (1966a). A similar phyllosoma 17 mm in length has recently been reported from the Indian Ocean by Saisho (1966b: 213, fig. 13). It seems a reasonable supposition that the above-mentioned palinurid phyllosomas, including the one referred to Scyllarides by Santucci, are larvae of Puerulus sewelli Ramadan, the type locality of which is the Gulf of Aden (see Holthuis, 1966).

W. von Bonde (1930) described a series of phyllosoma stages "all undoubtedly of the same genus and species," ranging in length from 4 to 17 mm. These he referred to Scyllarides elisabethae chiefly because it was the most common of the South African Scyllaridae and the only species of its genus known from South African waters. As Gurney (1936) correctly pointed out, von Bonde's material undoubtedly included larvae of more than one species. His specimens of 11 mm (pl. 6) and 17 mm (pl. 7) differ quite a bit

in morphology and both possess gill buds and other features characteristic of the final phyllosoma stage. It is difficult in fact to understand why von Bonde failed to realize that he was dealing with two specifically distinct forms. He resorted instead to a system of length measured between the third maxilliped ganglia and the last abdominal ganglia to account for discrepancies between the conventional total length and relative morphological development of what he believed to be successive stages of the same species. Gurney (1936) recognized that von Bonde's larva of 17 mm, with rounded fore-body and uropods, probably belonged to Scyllarus, but accepted von Bonde's identification of the specimen of 11 mm, which had a more or less trapezoidal fore-body and characteristic pointed uropods. It is now clear that this larva, as well as other larvae with pointed uropods attributed to Scyllarides, must belong to one or more Indo-West Pacific species of Scyllarus. Barnard (1950) recorded Scyllarus cultrifer (Ortm.), S. martensii Pfr., and S. tuberculatus (Bate) (= rugosus Milne Edwards) from South African waters.

Gurney (1936) believed that one of the larvae from the Red Sea described by Santucci (1927, pl. 3, fig. 1) as probably belonging to Thenus was actually Scyllarides, presumably because it had pointed uropods such as von Bonde had described. Santucci (1927) had distinguished a series of five stages (a-e) ranging in length from 6 to 18 mm, but illustrated only stage a (pl. 3, fig. 1) and parts of e

(pl. 3, figs. 2-4). He (p. 193) revised his earlier opinion (Santucci, 1926) concerning the larvae of Thenus, believing that these specimens from the Red Sea were Thenus rather than the form from the Mediterranean reported as Thenus by Stephensen (1923). Santucci's stages a-c cannot be accepted as larvae either of Thenus or Scyllarides; in my opinion they are late stages of a species of Scyllarus similar to those with pointed uropods reported from South Africa by von Bonde. Santucci's stage c, 9.5 to 10.7 mm in length, is probably the final phyllosoma, according to his description (p. 192) having gill buds. Santucci failed, however, to recognize it as such. Stages d and e, respectively 12.8-14.2 and 15-18 mm in length, are consistent with Prasad and Tampi's (1957) account of the larvae of Thenus orientalis (Rumphius) and were probably correctly referred to this genus by Santucci.

It now appears that the only larvae which can be accepted as Scyllarides prior to Gurney's (1936) study are the stage I phyllosomas from the Mediterranean described by Santucci (1925, 1928). Although Santucci's specimen from the pleopods of a female is imperfectly expanded, both it and his planktonic specimens from Messina agree in essential features with the stage I phyllosoma of Scyllarides aequinoctialis described herein. Among the most salient of these features from a generic point of view are the length and biramous nature of the antenna and the great length of pereiopod 3 relative to pereiopods 1 and 2. Gurney failed,

however, to appreciate their diagnostic significance in the stage I phyllosomas of *Scyllarides latus* reported by Santucci, and stated that "it is doubtful if these characters are sufficient to distinguish the genus from *Scyllarus*." He consequently believed that a stage I phyllosoma from Bermuda (p. 430, fig. 35) probably belonged to *Scyllarides* "since that genus alone is known from Bermuda, but its antennae are even shorter than those of *Scyllarus arctus*, and leg 3 is not strikingly longer than leg 2." As mentioned earlier, this specimen as well as the one designated "*Scyllarides* A" by Lebour (1950, fig. 3) appear to be identical with the stage I phyllosoma of *Scyllarus nearctus*. Lebour's "*Scyllarides* B" is consistent with the first phyllosoma of *Scyllarides aequinoctialis*, but could belong as well to *Scyllarides nodifer* or *Arctides guineensis*. The two specimens from the North Atlantic attributed to *Scyllarides* by Sims (1968) are larvae of *Scyllarus nearctus*.

F. Scyllarides nodifer (Stimpson)

Materials and methods. No larvae of this species were reared in the laboratory. Two ovigerous females obtained by Mr. William G. Lyons during the summer of 1967 were held in an aquarium, but unfortunately one died and the other tore off her eggs. I have examined 32 phyllosomas from the plankton, ranging in length from 6.2 to 36.7 mm, which I attribute to Scyllarides nodifer for reasons discussed herein. The collection data are given in Table 23. Most were taken in the Straits of Florida. Two late larvae were collected by R/V OREGON in the central Gulf of Mexico. A final phyllosoma 36.7 mm in length was taken off the northwest coast of Cuba. Another final phyllosoma captured in a plankton haul on 4 Feb. 1965 at G-505 was returned alive to the laboratory. The endopods of one side were broken off; those on the other side were intact. This specimen was maintained for two weeks in a large bowl at a temperature of about 24°C. Attempts were made to feed it brine shrimp nauplii and cut shrimp, but with little apparent success. The water was changed every second day. The animal died in the process of metamorphosis on the night of 17 Feb. The partially metamorphosed specimen and the still attached phyllosoma cuticle were preserved. Representative phyllosoma stages are deposited in the Invertebrate Museum of this Institute

TABLE 23

LIST OF STATIONS AT WHICH PHYLLOSOMAS OF *SCYLLARIDES NODIFER* WERE TAKEN

Station	Date (D/M/Y)	Position Lat. N	Position Long. W	Time	Gear	Gear depth(m)	Number of specimens	TL (mm)
G-43	20/VII/62	$25^{\circ}39'$	$79^{\circ}52'$-$80^{\circ}02'$	2026-2240	6' IKMT	87-139	1	7.0
G-53	28/VIII/62	$25^{\circ}32$-$40'$	$79^{\circ}32$-$43'$	2326-0325	6' IKMT	418	1	10.1
G-79	20/XII/62	$25^{\circ}39$-$42'$	$80^{\circ}03$-$05'$	1200-1302	6' IKMT	72-75	3	13.5-18.4
G-82	20/XII/62	$25^{\circ}32$-$47'$	$79^{\circ}50'$-$80^{\circ}03'$	1618-1816	6' IKMT	154	1	21.0
G-83	20/XII/62	$25^{\circ}47'$	$79^{\circ}47$-$50'$	1837-2039	6' IKMT	133-147	1	20.3
G-212	20/I/64	$23^{\circ}33.5$-$43'$	$82^{\circ}31$-$37'$	0539-0830	6' IKMT	855-863	1	36.7
G-505	4/II/65	$25^{\circ}39$-$53'$	$80^{\circ}00$-$01'$	1940-2020	2m plank. net	9	4	21.5-final
G-764	16/IX/65	$25^{\circ}10'$	$80^{\circ}06'$	0008-0040	3/4m plank. net	surface	18	6.2-19.0
OREGON-214	10/I/51	$25^{\circ}01'$	$89^{\circ}16'$	--	plank. net	--	2	26.4,30.2

(Acc. No. 32.3592).

Diagnosis of the Phyllosoma

Early stages with biramous antenna, pear-shaped fore-body, similar to other species of Scyllarides and related genera. Phyllosoma identifiable at TL 4-5 mm by rudimentary nature of bud of pereiopod 5; latter in intermediate stages remaining a small undeveloped bud, late in development becoming a short rudiment, with only a minute expod bud. Pereiopod 5 in final stage not longer than abdomen. Fore-body becoming more or less oval in outline, narrowing gradually toward anterior end. Length of final stage about 37 mm.

Characters of the Phyllosoma

The earliest stages are not known with certainty (see Sims, 1965a). They are probably similar to Scyllarides aequinoctialis.

The fore-body is pear-shaped in early stages. It becomes broader and more or less oval in outline later in development, tapering rather gradually toward the narrow anterior end. The fore-body is longer than wide and somewhat wider than the hind-body throughout development.

The abdomen in early stages is short and narrow. After the first few stages the posterolateral angles are without spines or setae. The posterior margin becomes rounded in

later stages as the telson develops. The abdomen becomes situated in the posterior concavity of the hind-body which begins to form at TL about 5 mm as the buds of pereiopod 5 begin to move away from the base of the abdomen. In the last stages the abdomen becomes well developed and the segments are marked off dorsally. Segments 4 and 5 develop a spiniform process at the midline of the posterodorsal margin which corresponds to a similar process on segments 4 and 5 in the postlarva of Scyllarides spp.

The eye probably becomes stalked in stage II. The eyestalk is 1.2-1.3 times the length of the antennule at TL 6-7 mm. In intermediate stages the ratio approaches 2.0, and in the last two stages is about 1.7.

The antennule is simple and unsegmented in the earliest stages, with a few terminal aesthetascs and a small seta medially slightly beyond the middle of its length. Between TL 4-6 mm the inner flagellum becomes differentiated as a short process, the outer flagellum becomes marked off from the peduncular portion, and the latter is differentiated into two segments. A third segment forms in the antennular peduncle at TL 12-14 mm. Aesthetascs are added in tufts along the distomedial edge of the outer flagellum as development progresses and the inner flagellum increases in length, becoming in the final stage more than half the length of the outer flagellum. The terminal article of the antennular peduncle in the final stage is somewhat shorter than the proximal two segments.

The antenna is biramous in early stages. The two rami are not articulated, but the basal portion of the endopod is articulated with a cylindrical apical segment which bears a few small terminal setae. Early in development the entire antenna becomes shorter and the relative size of the exopod decreases. At TL 11-12 mm an articulation marks off the endopod from the basal portion bearing the reduced exopod. In subsequent stages the antenna increases gradually in length, in the final stage extending slightly beyond the end of the antennule. The exopod is reduced in intermediate stages to a minute toothlike projection, which disappears entirely at TL about 20 mm, at which length the lateral process of the antenna first becomes differentiated as a small triangular projection at the outer distal end of the second article. The antenna becomes divided into five more or less differentiated segments, including the basal portion. The lateral process becomes progressively larger and in the final stage is much expanded. Both margins, as well as those of the terminal article of the antenna, are entire.

Maxilla 1 is biramous and has no palp. In early stages the coxal endite bears two stout, elongated terminal setae plus a few smaller terminal and subterminal spines or setae. Later in development a third, somewhat smaller terminal seta and several spines are added. The basal endite in early stages bears two strong terminal teeth plus a few smaller spines or setae. At TL about 5-6 mm a third terminal tooth develops. In subsequent stages a few additional subterminal

spines or setae appear. In some late-stage individuals the basal endite of one side may bear a fourth terminal tooth.

Maxilla 2 in early stages consists of a basal segment and a smaller, narrow apical article bearing four long, plumose setae. At TL 9-11 mm the setae are lost and the division between the two segments becomes obscure. The anterior margin of the basal portion bears two small setae distally and one proximally. In later stages the distal portion, representing the exopod, begins to expand. In the final stage it assumes the paddle-shaped form of the scaphognathite.

Maxilliped 1 is not present until TL about 12-13 mm, when it is just indicated as an elevation posterior to the base of maxilla 2. In subsequent stages it becomes a short bud, which in late stages shows signs of differentiation. In the final stage maxilliped 1 is a finger-like process with a large oval lobe laterally representing the epipodite.

Maxillipeds 2 and 3 each consist of five segments. The distal portion of the propodus of both maxillipeds and the dactyl of maxilliped 3 are provided with spines or setae which increase in number as development progresses. Both maxillipeds are without exopods in early stages, although the second segment of maxilliped 3 has on its outer side near the middle of its length a small bump which Sims (1965a) has termed the presumptive exopod. This becomes a small, rounded bud in the stage preceding the subfinal stage, and in the last stage is a short, slender rudiment without

setae. A swelling indicating the incipient exopod bud appears on the second segment of maxilliped 2 in a late stage. In the subfinal stage it is a minute protuberance, which in the final stage becomes a short, oval bud. A lobe representing the epipodite is attached at the distal end of the coxal segment of maxilliped 2 in the final stage.

Pereiopods 1 and 2 are no doubt well developed in stage 1 and possess a setose exopod. The number of pairs of natatory setae, which might be of value as a specific if not generic character, has not been determined. The exopod of pereiopod 3 probably acquires setae in stage III. Pereiopod 4 becomes differentiated early in development, with a setose exopod at TL about 4 mm. The number of pairs of setae on the exopods of pereiopods 1 and 2 probably increases by one per molt in the first few stages, but later it appears that more than one pair may be added at an ecdysis. In early stages a few setae are added to the exopods of pereiopods 3 and 4 at each molt, so that by TL 12-15 mm the number equals that of pereiopods 1 and 2. In the final stage each exopod bears 27-28 pairs of setae. The number for various stages is given in Table 24.

Pereiopod 5 is indicated as a minute bud at the base of the abdomen at TL about 3 mm and begins to move away from the base of the latter at TL 4-5 mm. In subsequent stages pereiopod 5 remains a small, undifferentiated bud. Not until TL 19-20 mm does it show much increase in length and become divided into two segments. In the stage preceding

the subfinal stage pereiopod 5 is a somewhat elongated rudiment with a clearly demarcated coxal segment. The rest of the appendage is more slender than the latter and is incompletely differentiated into four segments. A minute, rounded exopod bud is present dorsally. In the subfinal stage pereiopod 5 consists of six segments, including a small, obtuse dactyl, and extends well beyond the end of the telson, but in the final stage it does not extend quite to the posterior margin of the latter. The exopod in the final stage is only a small rudimentary bud at the distal end of the second segment.

Pereiopods 1 and 2 have a short, claw-like dactyl, that of pereiopod 2 being slightly the longer. The distal portion of the propodus of both pereiopods is provided with numerous spines or setae. After the early stages pereiopods 3 and 4 become longer and more robust than pereiopods 1 and 2. Pereiopod 3 has an elongated, blade-like dactyl, whereas the dactyl of pereiopod 4 is quite short, extending only slightly beyond the dilated distal end of the propodus. The latter lacks spines or setae. The lengths of the various segments of the pereiopods of the final phyllosoma which died in the process of metamorphosis are given in Table 25.

Coxal spines are present on pereiopods 1-3 in early stages. They become shorter but persist until TL about 9-10 mm, when they disappear entirely. No coxal spines are found in any later stage.

The uropods are indicated as slight swellings as early

as TL 13 mm, and appear as low folds at TL 15 mm. They soon become small lobes shallowly cleft at the tip, which at TL 20 mm are oval, biramous rudiments. The outer ramus, longer than the inner, extends to the posterior end of the telson. In subsequent stages the uropods become well developed, and in the last stages project beyond the end of the telson. The outer ramus is articulated at the base.

The pleopods are first indicated at TL about 18 mm as four pairs of low crescent-shaped folds. At TL 21 mm they are distinct buds. In subsequent stages they become biramous. In the final stage the pleopods are elongated and leaf-like; the endopod is slightly longer than the exopod, and there are indications of articulation to the protopodite. The incipient appendix interna is indicated in the subfinal stage as a small rounded protuberance on the medial side of the endopod, and in the final stage it becomes a short, free cylindrical process.

Gill buds are present only in the final stage. Their distribution is given in Table 26. A total of 19 are present on each side, not including any of the epipodites. As Ortmann (1893) pointed out, pereiopods 2-4 in the phyllosoma each have only one arthrobranch but two pleurobranchs, the latter located dorsally on the thorax, whereas in adult decapods these appendages have two arthrobranchs and one pleurobranch. It is clear that one of the larval pleurobranchs on these thoracic segments must later become an arthrobranch. Gilchrist (1916) also called attention to

the difference in the position of the gills in the phyllosoma and the adult, and by tracing them in the postlarval stage of Jasus lalandii was able to show that "The adult condition may therefore be described as brought about by the posterior pleurobranch of the phyllosoma becoming an arthrobranch in the adult."

Description of Illustrated Stages

Length 6.6 mm (fig. 83). G-764. Fore-body pear-shaped, nearly 1.7 times longer than wide, slightly wider than hind-body; latter shallowly concave posteriorly. Abdomen short, narrow, without spines, uropods or pleopods, extending beyond level of bases of pereiopod 4. Eyestalk 1.25 times length of antennule. Antennular peduncle with two segments, proximal twice length of distal. Outer flagellum marked off from peduncle; inner flagellum a short conical bud. Antenna short, biramous; basal portion of endopod articulated with small, cylindrical terminal segment; exopod a short pointed process. Maxilla 1 biramous, without palp; coxal endite with two stout, elongated terminal setae plus smaller spines or setae; basal endite with three strong terminal teeth, middle one smaller than others, plus a few spines or setae. Maxilla 2 consisting of basal segment and smaller apical article bearing four long, plumose setae; anterior margin of basal segment with two small setae distally and one proximally. Maxilliped 1 not indicated. Maxillipeds 2 and 3 each with five segments, without

exopod; second segment of maxilliped 3 with slight bump representing presumptive exopod bud. Pereiopods 1-4 well developed, with setose exopods. Pereiopod 5 a small rounded bud a short distance removed from base of abdomen. Pereiopods 1-3 with a short coxal spine.

Length 12.8 mm (fig. 84). G-764. Fore-body 1.6 times longer than wide, nearly 1.1 times wider than hind-body. Eyestalk about 1.5 times length of antennule. A third segment indicated in antennular peduncle. Antenna longer than first segment of antennular peduncle; an articulation between base of endopod and basal portion; latter with a small triangular process laterally representing reduced exopod. Basal endite of maxilla 1 with three equal terminal teeth. Maxilla 2 without apical setae. Maxilliped 1 faintly indicated as elevation posterior to base of maxilla 2. Pereiopods 1-4 without a coxal spine. Pereiopod 5 a small bud. Uropods indicated as slight swellings.

Length 18.4 mm (fig. 85). G-764. Fore-body 1.5 times longer than wide, nearly 1.2 times wider than hind-body. Eyestalk about twice length of antennule. Distal segment of antennular peduncle somewhat shorter than proximal two. Antenna longer than first two articles of antennular peduncle; exopod represented only by small toothlike projection at outer distal end of basal segment; remainder of antenna showing indications of division into four segments; incipient lateral process indicated by prominence at outer distal end of second article. Maxilla 2 somewhat shortened

but not much expanded. Maxilliped 1 a small bud. Pereiopod 5 a slightly elongated bud less than half length of abdomen. Uropods short lobes with trace of bifurcation at tip. Pleopods indicated as four pairs of low folds.

Length 26.6 mm (fig. 86). G-505. Fore-body rather oval in outline, about 1.4 times longer than wide, 1.2 times wider than hind-body. Abdomen extending beyond level of bases of pereiopod 4; segments indicated dorsally near midline; posterodorsal margin of segments 4 and 5 with a small toothlike projection in midline. Eyestalk nearly twice length of antennule. Antenna nearly as long as antennule, partially divided into five segments, including basal portion; latter without trace of exopod; second article with pointed triangular process at outer distal end. Distal portion of maxilla 2 somewhat broader than basal portion. Maxilliped 1 a short conical bud. Second segment of maxilliped 2 with slight swelling laterally representing incipient exopod bud. Second segment of maxilliped 3 with small but distinct exopod bud near middle of its length. Pereiopods 3 and 4 longer and more robust then pereiopods 1 and 2; dactyl of pereiopod 3 elongated, blade-like; dactyl of pereiopod 4 short, extending only slightly beyond distal end of propodus; latter without spines or setae. Pereiopod 5 an elongated rudiment extending nearly to end of telson; coxal segment clearly demarcated, remainder of appendage showing incomplete division into four segments; second segment with a minute, rounded exopod bud dorsally at distal end. Uropods

biramous; outer ramus extending to end of telson. Pleopods biramous rudiments.

Length 30.2 mm (fig. 87). Subfinal stage. OREGON-214. Fore-body more or less oval in outline, about 1.4 times longer than wide, 1.2 times wider than hind-body. Abdomen well developed; segments marked off dorsally, most completely near midline; a short blunt tubercle at posteroventral margin on each side of segments 2-4; posterodorsal margin at midline of segments 4 and 5 projected into an obtuse, triangular process, that of segment four the larger. Posterior margin of telson rounded. Eyestalk about 1.7 times length of antennule. Antenna as long as antennule, with five more or less distinct segments; second with a prominent triangular process. Coxal endite of maxilla 1 with two stout, elongated terminal setae and a third smaller but similar seta, plus several smaller terminal and subterminal spines or setae; basal endite of left maxilla 1 with four strong terminal teeth plus smaller spines or setae; basal endite of right side with three terminal teeth. Distal portion of maxilla 2 expanded. Maxilliped 1 a bud showing signs of differentiation. Second segment of maxilliped 2 with minute protuberance representing exopod bud. Second segment of maxilliped 3 with a small oval exopod bud. Pereiopod 3 in this specimen not much longer than pereiopods 1 and 2, perhaps having been regenerated. Pereiopod 5 extending well beyond end of telson, with six segments, including a small dactyl; coxal segment broader than rest of

appendage; second segment with a small exopod bud. Uropods well developed, oval; outer ramus articulated at base, extending beyond posterior margin of telson. Pleopods biramous; inner ramus with small rounded protuberance on medial side representing incipient appendix interna. No gill buds.

Length 36.7 mm (fig. 88). Final stage. G-212. Forebody more or less oval in outline, narrowing gradually toward anterior end, about 1.4 times longer than wide, 1.2 times wider than hind-body. Abdomen about 3/4 length of hind-body, tapering posteriorly; segments marked off dorsally, most completely near midline; posterolateral margin on each side of segment 5 drawn out posteriorly; a small spine or tubercle near posteroventral margin on each side of segments 2-5, that of segment 5 smaller than others; posterodorsal margin of segments 4 and 5 with a triangular, spiniform process at midline, that of segment 4 the larger. Eyestalk about 1.7 times length of antennule. First two articles of antennular peduncle somewhat longer than distal article; inner flagellum more than half length of outer flagellum; distomedial margin of latter provided with numerous aesthetascs. Antenna broad, slightly longer than antennule, with five more or less distinct segments; lateral process much expanded; inner and outer margins of latter and terminal article entire. Basal endite of maxilla 1 with three strong terminal teeth plus smaller subterminal spines or setae; coxal endite with three stout, elongated terminal setae plus several smaller terminal and subterminal spines or setae.

TABLE 24

NUMBER OF PAIRS OF NATATORY SETAE ON THE EXOPODS OF PEREIOPODS 1-4 IN VARIOUS PHYLLOSOMA STAGES OF SCYLLARIDES NODIFER

TL (mm)	Pereiopod 1	Pereiopod 2	Pereiopod 3	Pereiopod 4
6.6	12	12	11	8
7.5	12	13	12	10
10.1	16	16	16	14
12.8	17	18	17	16
15.3	19	20	20	19
18.4	22	24	24	23
19.0	21	22	22	21
21.0	23	24	24	23
26.6	26	25	26	25
30.2	27	28	28	27
36.7	27	28	28	28

TABLE 25

LENGTH IN MM OF THE VARIOUS SEGMENTS OF PEREIOPODS 1-4 IN THE FINAL PHYLLOSOMA OF SCYLLARIDES NODIFER

Pereiopod	Coxa	Basis	Ischiomerus	Carpus	Propodus	Dactyl
1	2.8	12.0	4.2	4.0	14.8	1.0
2	2.9	10.7	6.0	5.0	18.2	1.5
3	3.1	10.5	15.4	15.4	26.0	5.4
4	3.0	15.4	15.8	15.0	31.4	1.7

TABLE 26

DISTRIBUTION OF GILL BUDS IN THE FINAL PHYLLOSOMA OF *SCYLLARIDES NODIFER*

	Podobranch	Arthrobranch	Pleurobranch	Epipodite
Maxilliped 2	0	0	0	1
" 3	1	1	1	1
Pereiopod 1	1	1	1	1
" 2	1	1	2	1
" 3	1	1	2	1
" 4	1	1	2	1
" 5	0	0	1	0

Distal portion of maxilla 2 expanded in paddle-shaped form of scaphognathite. Maxilliped 1 a finger-like process with large oval lobe laterally representing epipodite. Second segment of maxilliped 2 with small oval exopod bud; coxal segment with epipodite attached at outer distal end. Second segment of maxilliped 3 with short, slender exopod rudiment. Pereiopod 5 not extending quite to posterior margin of telson, consisting of six segments including small, obtuse dactyl; second segment with small, rudimentary exopod bud. Uropods well developed, oval, extending beyond end of telson; outer ramus articulated at base. Pleopods elongated, leaf-like; endopod not much longer than exopod, with short, cylindrical rudiment of appendix interna medially. Gill buds present.

Discussion. The identity of this form of scyllarid phyllosoma has long been confused, it having been attributed first to Thenus and later to Parribacus. Previous work must be re-examined in the light of present findings.

A final phyllosoma similar to the one reported herein was described and illustrated by Ortmann (1893, pl. 7, fig. 3), who did not attempt to identify his specimen beyond assigning it to the Scyllaridae. This larva, which was collected in the South Atlantic Equatorial Current near Fernando Noronha, is larger than the present final-stage specimen, measuring 51 mm in length, and differs in certain other respects. Ortmann's figure shows pereiopod 5 to be nearly twice the length of the abdomen, whereas in the present

specimen it does not extend quite to the end of the telson. The fore-body appears to differ somewhat in its proportions, being broader toward the anterior end in Ortmann's specimen.

Stephensen (1923: 77, fig. 26) described and illustrated a phyllosoma 7 mm in length from the western Mediterranean which corresponds to the 6.6 mm larva illustrated herein. Since in the same work he had already assigned other larvae to the Mediterranean species *Scyllarus arctus* and *Scyllarides latus*, the only representatives of their genera known from that area at the time, Stephensen concluded that this specimen "must belong to the *Ibacus*-*Thenus* group." *Thenus orientalis* was the only species of this group ever reported from the Mediterranean. It is common in the western Indo-Pacific region, including the Red Sea, but its Mediterranean distribution consisted then, as well as today, of a questionable record by Babic (1913) of one specimen from the Adriatic Sea. On this basis, Stephensen with doubt identified the phyllosoma in question as "?*Thenus orientalis*."

Santucci (1926) reported a phyllosoma 30 mm in length from the Mediterranean having the same general features as those described herein. He pointed out the similarity of his specimen to the 7-mm larva described by Stephensen, and following the latter, designated his phyllosoma "?*Thenus orientalis*." The length of Santucci's specimen is somewhat greater than that of the phyllosomas in the present collection in a corresponding stage. Judged from the relative development of the various parts, Santucci's 30-mm larva

would require at least two additional stages to reach the final phyllosoma. The fore-body appears to be broader toward the anterior end than in the present specimens, thereby resembling Ortmann's 51-mm final stage.

Gurney (1936) studied 20 specimens of this form of phyllosoma ranging in length from 8 to 43 mm, collected at stations off the Atlantic coast of Africa and in the equatorial Atlantic north and south of St. Paul Rocks. He called attention to the difficulties in accepting the reference of this form to Thenus orientalis by Stephensen and Santucci, but provisionally accepted this identification "without conviction of its soundness." Gurney believed that his specimens did not belong to the same species as the larva described by Stephensen because the latter's figure showed strong coxal spines on pereiopods 1-3, whereas Gurney's larva of 8 mm (p. 433, fig. 38), as well as the later stages, lacked coxal spines. He thought, therefore, that "there must be two distinct species in the Mediterranean of the genus to which these larvae belong." In my opinion this is an unnecessary assumption, although Gurney's material may well have included larvae of more than one species. The coxal spines of the present 6.6-mm larva are lacking in slightly larger specimens, and Gurney's figure of the 8-mm specimen in fact shows a minute coxal spine on the left pereiopod 1. There is also a possibility that the size of the coxal spines in Stephensen's illustration may be somewhat exaggerated. The phyllosoma of 33 mm from the equatorial

Atlantic illustrated by Gurney (p. 436, fig. 40) is larger than the present specimens in a corresponding stage of development. Like Santucci's specimen from the Mediterranean, the fore-body is broad anteriorly and becomes narrow rather abruptly at the anterior end; the final phyllosoma of the species to which it belongs would probably be similar to the specimen of 51 mm reported by Ortmann.

Under the general characters of the phyllosoma, Gurney (p. 432) stated that the fore-body is about 1½ times as wide as long. This is erroneous, since at all stages of development the length of the fore-body is clearly greater than the width. His figure of the 33-mm phyllosoma shows pereiopod 3 with a short dactyl and pereiopod 4 with an elongated, blade-like dactyl. This is probably an error in illustration, or the pereiopods may have been detached from the larva, since in his fig. 39d the dactyl of pereiopod 4 is short. Santucci's illustration of a similar larva shows the dactyl of pereiopod 3 to be longer than that of pereiopod 4, as in the present specimens.

Sims (1964) mentioned large numbers of phyllosoma larvae 1.2 to 29.2 mm in length collected in the western Atlantic "which seem to be of the same species as Gurney's Thenus?" He mentioned that Dr. L. B. Holthuis had examined samples of these phyllosomas, was doubtful that they were Thenus, and thought "that they might possibly belong to the newly erected genus Arctides." According to Sims, Holthuis suggested also that they might belong to the genus Parribacus.

In his 1965a paper, Sims attributed a sequence of 12 phyllosoma stages from the western Atlantic to Parribacus sp. The stages designated 4-10 appear to belong to the same species as the larvae described herein, having the characteristic rudimentary pereiopod 5. Some of the earlier stages in his sequence are probably of the same identity, while others perhaps are not. The size range given in Tabel 2 by Sims for the first one or two stages seems excessive; phyllosomas of more than one genus or species may have been included. A careful comparison will be necessary to recognize specific or even generic characters among the early stages (under TL 4-5 mm) of scyllarid phyllosomas having a biramous antenna and pear-shaped fore-body. Once the persistent rudimentary nature of the bud of pereiopod 5 becomes evident, as in Sims' stage 5, this phyllosoma can be readily distinguished from similar forms in which pereiopod 5 becomes well developed, with a functional exopod, at a relatively early stage.

It is now clear that the last two stages (11 and 12) of Sims' sequence, which have pereiopod 5 well developed and with a setose exopod, do not belong to the same species as his stages 4-10. Sims' material apparently did not include the last two stages of the form in which pereiopod 5 remains rudimentary; hence he erroneously completed his sequence with two stages of a similar but distinctly different species of phyllosoma.

Sims (1965a) correctly pointed out that phyllosomas

of the form with which he was dealing could not belong to the genus *Thenus* as earlier investigators has supposed. This had become clear when Prasad and Tampi (1957) demonstrated the true characters of the larvae of this genus by hatching the first phyllosoma of *Thenus orientalis* from the egg and linking it with later stages taken from plankton in the Indian Ocean. Sims' reasons for identifying his material as *Parribacus* are discussed in the present study under the section dealing with the latter. This seemed to be a reasonable identification on the basis of the available evidence, although there were certain difficulties which are pointed out below. *Scyllarides* could hardly be considered as the parent of the larvae in question, since previous accounts of larvae of that genus depicted a phyllosoma closely resembling those known to belong to *Scyllarus* and having long telson spines or pointed uropods.

The generic identity of the phyllosomas having the rudimentary pereiopod 5 can be determined with certainty by rearing larvae of known parentage to a stage at which the persistent rudimentary nature of the bud of pereiopod 5 becomes evident. A considerable body of indirect evedence is now available which indicates that the western Atlantic phyllosomas described herein are larvae of *Scyllarides nodifer*. This evidence may be summarized as follows:

(1) The phyllosomas are similar in morphology to those which are now known to belong to *Scyllarides aequinoctialis*. The chief points of difference are the rudimentary nature of

pereiopod 5 throughout development, the shorter dactyl of pereiopod 4 and the more gradual narrowing of the fore-body toward its anterior end.

(2) Postlarvae of Parribacus as reported by Boas (1880), Rathbun (1906) and Parisi (1917) measure 50 mm or more in total length and over 20 mm in carapace length. Postlarvae of this size could not be produced from a final phyllosoma of the size attributed by Sims to Parribacus, there being a considerable reduction in total length at metamorphosis resulting from the fusion of the elongated fore-body with the hind-body to form the cephalothorax. The partially metamorphosed postlarva obtained in the present study from a final phyllosoma having the rudimentary pereiopod 5 agrees in size and in those definitive features which are evident with postlarvae known to belong to Scyllarides spp.

(3) A further objection to Sims' identification of the phyllosomas as Parribacus was that adults of that genus, known in the western Atlantic from Florida to Brazil, have never been reported from the eastern Atlantic or Mediterranean Sea, where there are found phyllosomas almost certainly belonging to the same genus as the western Atlantic larvae. Sims (1968) recently reported as Parribacus a larva of this form collected near the Azores. Later stages of the form from the Mediterranean and eastern and equatorial Atlantic differ somewhat from the western North Atlantic form described herein in size and in certain proportions of the fore-body, indicating that there are at least two different

species in the Atlantic having this type of phyllosoma. This casts doubt upon the possibility that the phyllosomas could be larvae either of Parribacus or Arctides, since both of these genera are represented in the Atlantic by a single known species. Scyllarides is the only other genus of Scyllaridae other than Scyllarus known from the western Atlantic, where it is represented by five species. Scyllarides is represented also in the eastern Atlantic and Mediterranean Sea, and at the island of St. Helena in the South Atlantic.

(4) Another difficulty in accepting the identification of these phyllosomas as Parribacus is that Sims' studies on the distribution of the larvae indicated "that adult populations must occur in the Gulf of Mexico and Atlantic Ocean as well as the Caribbean Sea." As Sims acknowledged, "Such populations have not been found or reported." The larval distribution agrees with the known distribution of adults of Scyllarides nodifer, which is found at Bermuda and from Cape Lookout, North Carolina to Cuba and in the Gulf of Mexico (Williams, 1965). To my knowledge Scyllarides nodifer is the only scyllarid lobster other than species of Scyllarus which is commonly found in the Gulf of Mexico.

(5) As shown earlier, the long telson spines thought by Stephensen (1923) to be characteristic of the larvae of Scyllarides latus are probably a feature of the phyllosomas of Scyllarus pygmaeus. It is therefore highly probable that the phyllosomas from the Mediterranean which Stephensen (1923) and Santucci (1926) referred to Thenus belong instead

to *Scyllarides latus*, the only scyllarid lobster other than the two species of *Scyllarus* known with certainty to occur in the Mediterranean Sea. The phyllosomas from the Mediterranean as well as those from the equatorial Atlantic resemble the ones described herein and differ from *S. aequinoctialis* in having a rudimentary pereiopod 5. This is consistent with the affinities recognized within the genus; on the basis of adult morphology *S. latus* is more closely allied to *S. nodifer*, *S. herklotsii* and *S. delfosi* than to *S. aequinoctialis*. Verrill (1922) and Holthuis (1946) remarked that *Scyllarides americanus* (= S. *nodifer*) was perhaps only a subspecies of *S. latus*.

As shown previously, the duration of each of the early stages of *Scyllarides aequinoctialis* at 24 ± 1°C was about 8-11 days. Saisho (1962b) reported a comparable period for the first two stages of *Parribacus antarcticus*. Although larvae of *Scyllarides nodifer* cannot be assumed to have a similar duration, I consider it likely that they do. The duration of the later stages is probably somewhat longer, but the extent of increase is difficult to assess. The lower water temperatures prevailing in the winter months during which the later stages occur probably contribute to lengthening the duration. The final phyllosoma captured alive on 4 Feb. 1965 died in the process of metamorphosis on 17 Feb., which suggests a duration of at least two weeks for the final stage even at a relatively warm temperature (24°C). It is not possible to know, however, how long the larva was

in the final stage prior to capture, nor how it may have been affected by laboratory conditions and lack of suitable food.

Data collected by Sims (1965a) on the monthly size progression of the various phyllosoma stages indicated the length of larval life to be about nine months; however, the last two stages upon which this estimate was based, as shown herein, do not belong to the same species as the earlier stages.

Sims found stage I phyllosomas possibly belonging to this species in April and August in the Yucatan and Florida Straits. The seasonal size progression of later stages in the Straits of Florida was variable, whereas an increasing progression was found in the area of the Dry Tortugas and Florida Keys. The present limited data provide only a fragmentary picture of the distribution of the various stages. They do indicate a steady seasonal progression in size (Table 27) which may or may not be significant. From nearly the same locality in the Straits of Florida opposite Miami, individuals of TL 7.0 and 10.1 mm were taken respectively in July and August, 1962; 18 specimens of mean length 12.6 mm in September, 1965; five phyllosomas of mean length 18.2 mm in December, 1962; and four larvae of mean length 29.4 mm, including one final stage, were collected on 4 Feb. 1965. The only other final phyllosoma was captured off the northwest coast of Cuba on 20 Jan. 1964. Three postlarvae believed to belong to Scyllarides nodifer (William G. Lyons, unpublished manuscript) were collected with night light and

TABLE 27

SEASONAL DISTRIBUTION OF PHYLLOSOMAS OF SCYLLARIDES NODIFER IN THE STRAITS OF FLORIDA

Date		Number of Larvae	Length (mm)	Mean Length (mm)
20 July	1962	1	7.0	----
28 Aug.	1962	1	10.1	----
16 Sept.	1965	18	6.2-19.0	12.6
20 Dec.	1962	5	13.5-21.0	18.2
4 Feb.	1965	4	26.6-36.7 (app)	29.4

dipnet off the pier of this Institute, one in March 1965 and two in late Feb. 1966. The occurrence of the final phyllosoma in January and February suggests a larval life of six to ten months, depending on the time of hatching and temperature.

Ovigerous females of _Scyllarides_ _nodifer_ occur primarily from June to August in the eastern Gulf of Mexico, being most frequent in June (William G. Lyons, personal communication). Sims (1965a) found stage I phyllosomas in the Gulf of Mexico during June. Late phyllosomas 26.6 and 30.2 mm in length were taken in the central Gulf of Mexico on 10 Jan. 1951 by R/V OREGON, suggesting a larval life of eight or nine months.

G. *Parribacus antarcticus* (Lund)

Materials and methods. I have examined seven specimens of this phyllosoma, ranging in length from 8.5 to 65 mm, from plankton in the western Atlantic. I attribute them to *Parribacus antarcticus* for reasons discussed herein. The collection data are given in Table 28. The smallest larva was taken in the Straits of Florida between Florida and the Bahamas. Two specimens 11.3 and 13 mm in length were collected by R/V JOHN ELLIOTT PILLSBURY northeast of the northern Bahamas; a specimen of 19.4 mm in the collection of the USNM was probably taken in the same general area. A specimen 24 mm in length was collected in the South Atlantic off Recife, Brazil by the U. S. Fish and Wildlife Service R/V UNDAUNTED. Through the courtesy of the staff of the Florida State Board of Conservation Marine Laboratory I have been able to examine the specimen of 36.5 mm from the Straits of Florida (23° 14'N, 83° 48' W) described as "Phyllosome D" by Sims (1964: 263, fig. 4). The largest specimen was collected in the Caribbean Sea near Grand Cayman Island by R/V CHAIN of the Woods Hole Oceanographic Institution. I have also had the opportunity to examine two of the three specimens reported by Gurney (1936) from the DISCOVERY collection.

The 65-mm larva will be deposited at the Woods Hole Oceanographic Institution; the 24-mm larva at the Tropical

TABLE 28

LIST OF STATIONS AT WHICH PHYLLOSOMAS OF PARRIBACUS ANTARCTICUS WERE TAKEN

Station	Date (D/M/Y)	Time	Position Lat.	Position Long.	Gear	Gear depth(m)	TL mm
R/V GERDA SL20 B3	8/X/53	0215	$25^{\circ}35'$N	$79^{\circ}25'$W	3/4m plank. net	276	8.5
R/V PILLSBURY 164	7/VIII/64	2115-2215	$28^{\circ}27'$N	$73^{\circ}39'$W	2m plank. net	2	11.3,13
R/V GRAMPUS 10196	3/III/14	--	--	--	plank. net	sfc	19.4
R/V UNDAUNTED 5-136	8/IX/66	1815	$08^{\circ}07'$S	$33^{\circ}00'$W	ICITA net	--	24
Y211b	19/XII/62	2130	$23^{\circ}14'$N	$83^{\circ}48'$W	1/2m plank. net	sfc	36.5*
R/V CHAIN 60	9/VI/66	2025-2300	$19^{\circ}40$-$46'$N	$82^{\circ}58'$-$83^{\circ}07'$W	6' IKMT	subsfc	65

*"Phyllosome D," reported by Sims (1964)

Atlantic Biological Laboratory, Miami, Florida; and the specimens of 8.5, 11.3 and 13 mm at this Institute (Acc. No. 32.3370). The specimen described by Sims is deposited at the Florida State Board of Conservation Marine Laboratory, St. Petersburg, Florida. The two specimens reported by Gurney are now at the National Institute of Oceanography, Wormley, Godalming, Surrey, England.

Diagnosis of the Phyllosoma

Stage I 1.5-1.6 mm in length; exopod of pereiopods 1 and 2 with five pairs of natatory setae; early stages with biramous antenna, pear-shaped fore-body, similar to Scyllarides and probably Arctides. Pereiopod 5 becoming well developed at relatively early stage, with setose exopod by TL 9-10 mm. Endopod of antenna losing articulation and exopod disappearing entirely by TL about 9 mm; antenna in subsequent stages up to TL nearly 35 mm uniramous, without indication of lateral process. Fore-body in early stages slightly wider than hind-body, becoming in later stages progressively broader anteriorly and increasingly wider than hind-body. Phyllosoma attaining great size; length of final stage 75-80 mm.

Characters of the Phyllosoma

The first three stages of Parribacus antarcticus have been described from laboratory reared material by Saisho

(1962b, 1966b). These larvae possess the same general characteristics, i. e. biramous antenna and pear-shaped fore-body, as the early stages of Scyllarides aequinoctialis. They doubtless are similar also to other species of Scyllarides and to the form tentatively identified in the present study as Arctides guineensis. Stage I of Parribacus antarcticus appears to differ from stage I of Scyllarides aequinoctialis chiefly by its smaller size (TL 1.54-1.60 mm) and by possessing only five pairs of natatory setae on the exopods of pereiopods 1-2. A direct comparison might reveal other differences. The first phyllosoma of Parribacus was earlier described from laboratory hatched material by Aikawa and Isobe (1955). They reported a total body length of 1.8 mm, and that maxilliped 1 "is wholly absent;" however, the mouthparts are misidentified in their confused description. According to Saisho (1962b), maxilliped 1 "is a mere stump-like projection immediately behind the base of the second maxilla." He apparently did not attempt to explain this discrepancy or the difference in length.

Stage III of P. antarcticus according to Saisho measures 2.6-2.8 mm in length; the pear-shaped fore-body is more than 1.3 times longer than wide and nearly 1.2 times wider than the hind-body. Its posterolateral margins cover all or part of the bases of maxilliped 3. The phyllosoma at this stage unfortunately does not exhibit any definitive features that would permit a positive identification of later stages from the plankton. The identity of the later stages described

herein could probably be conclusively demonstrated by rearing phyllosomas of P. antarcticus to the most advanced stage possible.

In the 8.5 mm specimen the pear-shaped fore-body has become relatively longer and its width relative to the hind-body has decreased. The fore-body is about 1.5 times longer than wide and only slightly wider than the hind-body. In subsequent stages the fore-body gradually increases in width and becomes progressively broader anteriorly. At TL 65 mm it is only 1.1 times longer than wide and nearly 1.4 times wider than the hind-body. At a length somewhere under 8.5 mm the posterolateral margins of the fore-body no longer cover the bases of maxilliped 3, and not until TL about 37 mm do they again cover the latter. At TL 65 mm they cross the hind-body between the bases of maxilliped 3 and pereiopod 1.

The hind-body between stage III and TL 8.5 mm becomes broader and assumes a characteristic outline which it retains throughout subsequent development. A posterior concavity in which the abdomen is situated forms as the rudiment of pereiopod 5 moves away from the base of the abdomen. The latter in early stages is narrow and more or less parallel-sided, with a short spine and three small setae at each posterolateral angle. By TL 8.5 mm the spines have disappeared. In later stages the telson becomes rounded posteriorly. At TL 65 mm it is slightly indented at the midline. At TL 8.5 mm the abdomen extends to the level of the

base of pereiopod 5. In subsequent stages it is situated within the depression of the hind-body and does not extend to or beyond this level until late in development. At TL 65 mm the abdomen is not quite half the length of the hind-body and the segments are marked off dorsally near the midline. Segments 2-5 have a short, blunt spine or tubercle on each side at the posteroventral margin. There are no spines at the posterodorsal margin of any segment.

The eye in stage I is not stalked. A stalk is marked off in stage II, which in subsequent stages increases gradually in length. Between TL 8.5 and 13 mm the eyestalk is about 1.5 times the length of the antennule. In intermediate stages this ratio increases slightly to 1.6, and at TL 65 mm is again about 1.5.

The antennule is simple and unsegmented in the earliest stages. By TL 8.5 mm the peduncular portion is clearly marked off from the flagellum and consists of two distinct segments. A third article appears at TL 11-13 mm. In intermediate and late stages there is not much difference in the lengths of the three segments; the second may be slightly the longest.

The antenna in stage I is biramous and slightly shorter than the antennule. The endopod has an articulation. In the stages between III and TL 8.5 mm the antenna becomes shorter and is considerably modified in form. Its mode of development differs from that observed in Scyllarides and in the phyllosoma tentatively identified as Arctides in

that the exopod at TL 8.5 mm is reduced to a small rounded protuberance, which by TL 11 mm has disappeared entirely. Moreover, the articulation in the endopod shifts to the distal extremity or disappears entirely by TL 8.5 mm. There is no articulation in the antenna in subsequent stages as it increases gradually in length. Indications of a division into four articles are visible beneath the cuticle by TL 19 mm, but there is no external segmentation. A lateral process does not appear until TL 37 mm, at which length it is represented by a small obtuse protuberance at the distal end of the second incipient article. At TL 65 mm the antenna is slightly shorter than the antennule and still shows a partial division into four segments, the articulation distal to the lateral process being the most distinct. Both margins of the terminal article and the outer margin of the triangular process are shallowly crenulate beneath the cuticle, which suggests that they may show some degree of incision in the final phyllosoma stage.

Maxilla 1 is biramous, without palp. The coxal endite bears two stout, elongated terminal setae plus smaller terminal and subterminal spines or setae, the latter increasing in number as development progresses. The basal endite in early stages has two strong terminal teeth plus a few smaller spines or setae. In intermediate stages there is a third terminal tooth, which may appear as early as TL 11 mm, and at TL 65 mm three or four terminal teeth are present.

Maxilla 2 in stage I consists of an elongated basal

segment and a smaller, narrow apical article bearing four long, plumose setae. Two short setae are situated along the anterior margin of the basal segment, according to Saisho's figure. By TL 8.5 mm the apical segment and plumose setae have disappeared entirely. In intermediate stages maxilla 2 becomes somewhat shortened. By TL 37 mm the distal portion has begun to expand but is still narrower than the basal portion. At TL 65 mm the distal portion is expanded and broader than the latter.

Maxilliped 1, according to Saisho, is present in stage I as a small projection. It is not indicated in the 8.5-mm larva, but by TL 24 mm it appears as a slight elevation posterior to the base of maxilla 2. At TL 37 mm maxilliped 1 is a conical bud, which at TL 65 mm is larger and shows signs of differentiation.

Maxilliped 2 consists of five segments and is without an exopod bud until the last stages. At TL 65 mm the exopod bud is indicated as a slight protuberance on the second segment. Maxilliped 3 also consists of five segments, the second of which from the earliest stages has a slight bump laterally representing the presumptive exopod bud. This shows no differentiation until late in development; at TL 65 mm the exopod is a small, distinct rounded bud.

Pereiopods 1-3 are well developed in stage I; pereiopod 4 is indicated as a minute bud at the base of the abdomen. The exopods of pereiopods 1 and 2 each bear five pairs of natatory setae. The exopod of pereiopod 3 is a short,

rudimentary bud, which acquires natatory setae in stage III. Pereiopod 4 becomes well developed after the first few stages, with a functional exopod. Pereiopod 5 is indicated in stage III as a small bud at the base of the abdomen. At TL 8.5 mm it appears as an elongated rudiment about four times the length of the abdomen, with a somewhat elongated, rudimentary exopod bud. Between TL 9-10 mm the exopod acquires natatory setae, and the endopod soon becomes well developed. It appears that in intermediate and late stages a few pairs of natatory setae may be added to the exopods at an ecdysis. At TL 65 mm the exopods of pereiopods 1-4 each bear 57 pairs of natatory setae. The number of pairs in various stages is given in Table 29.

In early stages pereiopods 1-3 have a prominent coxal spine with an accessory seta at its base. By TL 8.5 mm the coxal spines are short and inconspicuous, and by TL 11 mm they have entirely disappeared. No coxal spines are present in subsequent stages.

The endopods are broken off in the present specimens, but in the larva 70 mm in length from the Marshall Islands described by Johnson (1951), which almost certainly belongs to the same genus, the pereiopods are intact. In this specimen pereiopods 3-5 are considerably longer than pereiopods 1-2. The dactyls of the latter are short and claw-like, whereas those of pereiopods 3-4 are much elongated, slender, and sickle-shaped. The dactyl of pereiopod 5 is short but differs in form from that of pereiopods 1-2; it resembles

TABLE 29

NUMBER OF PAIRS OF NATATORY SETAE ON THE EXOPODS OF PEREIOPODS 1-5 IN VARIOUS PHYLLOSOMA STAGES OF *PARRIBACUS ANTARCTICUS*

TL (mm)	P. 1	P. 2	P. 3	P. 4	P. 5
8.5	--	13	13	11	0
11.3	18½	20	18	15	8½
13.0	19½	21	19	16½	10
19.4	27	28	26	24	20
24	33	35	32	32	27
36.5*	42	44	42	41	38½
65	57	57	57	57	--

* "Phyllosome D," reported by Sims (1964).

the dactyl of pereiopod 4 of *Scyllarides aequinoctialis* described in the present study.

The uropods are faintly indicated beneath the cuticle at TL 11-13 mm, and at 19 mm appear as low, undifferentiated folds. By TL 37 mm they have become short, biramous rudiments; the outer ramus is longer than the inner but does not extend to the end of the telson. At TL 65 mm the uropods are well developed and oval in outline. The exopod, slightly longer than the endopod, is articulated at the base and extends slightly beyond the posterior margin of the telson.

The pleopods by TL 24 mm are indicated as four pairs of low folds in the cuticle, which by TL 37 mm have become slightly elongated, uniramous buds. At TL 65 mm the

pleopods are biramous and project laterally beyond the margins of the abdomen at a characteristic angle. The endopod is slightly longer than the exopod, with the incipient appendix interna indicated medially beneath the cuticle.

No gill buds are present in the 65-mm specimen. In view of its size and relatively advanced morphological development, it seems highly probable that it represents the subfinal phyllosoma stage. The final phyllosoma, judged from the report of Prasad and Tampi (1965), is probably about 75-80 mm in length.

Description of Illustrated Stages

Length 8.5 mm (fig. 92). Fore-body pear-shaped, 1.5 times longer than wide, slightly wider than hind-body, narrowing gradually toward anterior end; posterolateral margins not covering base of maxilliped 3. Abdomen without spines, uropods or pleopods, situated in posterior concavity of hind-body, extending to level of base of pereiopod 5. Eyestalk nearly 1.5 times length of antennule. Antennular peduncle with two distinct segments; inner flagellum a short process; outer flagellum clearly marked off from peduncular portion. Antenna less than 1/3 length of antennule, possibly with indication of articulation near distal end; a small, rounded process on outer side at about middle of its length. Maxilla 1 biramous, without palp; coxal endite with two stout, elongated terminal setae plus

a few smaller spines or setae; basal endite with two strong terminal teeth plus a few smaller spines or setae. Maxilla 2 a single segment without terminal setae; anterior margin with two small setae. Maxilliped 1 not indicated. Maxillipeds 2 and 3 each with five segments, without exopod. Pereiopods 1-4 well developed; exopod of pereiopod 1 missing; those of pereiopods 2-4 respectively with 13, 13 and 11 pairs of natatory setae. Pereiopod 5 a rudiment about four times length of abdomen; coxal segment clearly demarcated, remainder of appendage with traces of segmentation; exopod a somewhat elongated rudiment without setae. Pereiopods 1-3 with a short, inconspicuous coxal spine.

Length 13 mm (fig. 93). Fore-body somewhat broader anteriorly than in 8.5 mm larva; posterolateral margins not covering base of maxilliped 3. Abdomen not extending to level of base of pereiopod 5. Antennular peduncle with three segments. Antenna extending beyond end of first article of antennular peduncle, without segmentation and with no indication of an outer process. Pereiopod 5 smaller than pereiopods 1-4, but with setose exopod; exopods of pereiopods 1-5 respectively with 19½, 21, 19, 16½ and 10 pairs of natatory setae. No coxal spines present. Uropods faintly indicated beneath cuticle.

Length 24 mm (fig. 94). Fore-body 1.3 times longer than wide, more than 1.1 times wider than hind-body; broader anteriorly than in 13 mm stage; maximum width near middle of length; posterolateral margins not quite covering base

of maxilliped 3. Abdomen little developed, situated in posterior concavity of hind-body. Eyestalk about 1.6 times length of antennule. Antenna extending nearly to end of second article of antennular peduncle, with no outer process and no external segmentation, but division into four articles indicated beneath cuticle. Basal endite of maxilla 1 with three strong terminal teeth. Maxilla 2 short; distal portion not expanded. Maxilliped 1 indicated as slight elevation posterior to base of maxilla 2. Exopods of pereiopods 1-5 respectively with 33, 35, 32, 32 and 27 pairs of natatory setae. Uropods low, undifferentiated lobes. Pleopods indicated as four pairs of low folds in cuticle.

Length 65 mm (fig. 95). Fore-body broad, apple-shaped, 1.1 times longer than wide, nearly 1.4 times wider than hind-body, with greatest width somewhat anterior to middle of length, narrowing gradually toward rounded anterior margins, latter not projecting much anteriorly in form of "shoulders;" posterolateral margins crossing hind-body between base of maxilliped 3 and pereiopod 1. Abdomen slightly less than half width of hind-body, situated in concavity of latter, extending beyond level of base of pereiopod 5. Abdominal segments marked off dorsally near midline; segments 2-5 with a short blunt spine or tubercle on each side at posteroventral margin. No spines dorsally on any segment. Telson without spines; posterior margin slightly indented at midline. Eyestalk about 1.5

times length of antennule. Segments of antennular peduncle subequal in length. Antenna slightly shorter than antennule; not segmented externally but showing division into four articles beneath cuticle; second article with a prominent triangular process laterally; margins of terminal article and outer margin of triangular process shallowly crenulate beneath cuticle. Maxilla 1 biramous, without palp; coxal endite with two stout, elongated terminal setae and several smaller terminal and subterminal spines or setae; basal endite of left side with four strong terminal teeth plus smaller spines or setae; that of right side with three terminal teeth. Distal portion of maxilla 2, representing exopod, somewhat expanded, broader than basal portion. Maxilliped 1 a short bud showing indications of differentiation. Second segment of maxilliped 2 with a slight protuberance representing incipient exopod bud. Second segment of maxilliped 3 with a small, rounded exopod bud. Exopods of pereiopods 1-4 each with 57 pairs of natatory setae; exopod of pereiopod 5 fully developed but broken. Uropods well developed, oval, without spines; outer ramus articulated at base, slightly longer than inner ramus, extending slightly beyond posterior margin of telson. Pleopods biramous, projecting laterally beyond margins of abdomen at characteristic angle; endopod slightly longer than exopod, with incipient appendix interna indicated medially beneath cuticle. No gill buds present.

Discussion. Phyllosomas of the form described herein

have been reported on several occasions from the Indo-West Pacific region, but were previously known from the Atlantic only by single specimens recorded by Gurney (1936) and Sims (1964). One of the first phyllosomas on record, the *Cancer cassideus* of Forster (1781) from the "mari Indico," although not accurately illustrated, appears to be of this form. Guerin (1830) reported a specimen of 70 mm (*Phyllosoma laticornis* Leach) from the New Guinea area, and mentioned (Guerin, 1833) that smaller specimens (known under the name *Phyllosoma brevicornis* Leach) were rather common, being found in waters of Africa, New-Holland and the "Grandes-Indes." Milne-Edwards (1837) recorded five species apparently representing different stages of this phyllosoma under his Phyllosomes brevicaudes; the specimens were taken in the Indian Ocean and in Asian waters. Richters (1873) dealt with specimens from the Pacific.

A phyllosoma 15 mm in length which appears to belong to the same species as those described in the present study was reported from the South Atlantic south of St. Paul Rocks by Gurney (1936: 438, fig. 42). He tentatively referred to *Parribacus* this specimen and two larger, similar phyllosomas from the Indian Ocean off the east coast of Africa. I have examined the latter two specimens, 20 and 37 mm in length, and can verify Gurney's observation that they are not distinguishable from the Atlantic material. The specimen of 36.5 mm from the Straits of Florida described as "Phyllosome D" by Sims (1964) agrees in all respects with Gurney's

largest specimen. In giving the general characters of the phyllosoma, Gurney (p. 437) stated, "Fore-body pear-shaped, narrow in front, narrower than hind-body." The last observation is inexplicable, since his illustration of the 15-mm larva shows the maximum width of the fore-body to be slightly greater than that of the hind-body, and in his larger specimens the fore-body is unmistakably wider than the hind-body. Gurney suggested that a phyllosoma 30 mm in length reported from the West Indies by Bate (1888: 94, pl. 120, fig. 1) might belong to the same species as the abovementioned larva, but Bate's specimen clearly is of the form attributed in the present study to Arctides, having a fore-body distinctly narrower than the hind-body.

It is unfortunate that "an incident" prevented Saisho from rearing larvae of Parribacus antarcticus to a more advanced stage in which there might have become evident certain more definitive characteristics that would permit a positive identification of later stages from the plankton. Sims (1965a) attributed to Parribacus a sequence of 12 phyllosoma stages from plankton collected in the western Atlantic which are quite different from those described by Gurney under the designation "Parribacus?" Sims apparently based the identification of his material primarily upon: (1) a personal communication from Dr. Saisho, who stated after a direct comparison of some of Sims' early stages with the reared stages of Parribacus antarcticus, as cited by Sims (p. 163), "The smallest phyllosomas are surely the

first stage of *Parribacus* **and the** other advanced ones are, though there is no evidence, also of the same genus, I believe;" and (2) what appears to me to be a misinterpretation of a statement by Gurney. Sims (1965a), with reference to Gurney's (1936) summary, stated (p. 162) that the latter suggested that larvae which he had doubtfully designated *Thenus*(?) "may rightfully belong to the genus *Parribacus*, but his treatment of the entire subject is difficult to interpret." Sims apparently referred to p. 439 of Gurney's paper, on which is considered the possible identity of the phyllosomas described and discussed under the heading "Genus *Parribacus* Dana?" In the last paragraph on p. 439 Gurney stated, "The genus *Thenus* must be excluded if its phyllosoma is as described above;" and in the final sentence he suggested that it was "a reasonable guess" that *Parribacus ursus* (= *P. antarcticus*) "may be the parent of the Phyllosoma in question." In my understanding, Gurney's mention of the phyllosoma of *Thenus* "described above" was in reference not to the immediately preceding description on pp. 437-439, but to his earlier treatment on pp. 432-436 of the larvae which he doubtfully referred to "*Thenus* (?)," and that the "Phyllosoma in question" which he suggested might belong to Parribacus refers only to the form discussed on pp. 437-439. I therefore do not believe Gurney meant that the larvae which he had earlier designated "*Thenus* sp.?" might belong instead to *Parribacus* as Sims has asserted, but only that if the phyllosomas described

on pp. 432-436 really belonged to Thenus, then the latter had to be excluded from consideration as the parent of the larvae dealt with on pp. 437-439. The fact that fig. 41 illustrating parts of "Thenus sp.?" appeared on p. 437 under the heading Parribacus perhaps contributed to the confusion.

As mentioned earlier, Sims (1965a) correctly pointed out that phyllosomas of the form with which he was dealing could not belong to the genus Thenus as earlier investigators had supposed. There were difficulties, however, in accepting Sims' identification of his material as Parribacus. These have been pointed out in the present study under Scyllarides nodifer. As shown therein and in the section dealing with Scyllarides aequinoctialis, the identification of Sims' phyllosomas as Parribacus cannot be accepted. The early and intermediate stages (4-10) of his sequence belong in all probability to Scyllarides nodifer, and the last two stages (11-12) to Scyllarides aequinoctialis. The two phyllosomas collected in the North Atlantic off the coast of the United States, reported by Sims (1968) as Parribacus, probably belong to S. nodifer; a third specimen collected near the Azores may belong to S. latus.

In my opinion, the available evidence indicates Gurney's identification of the phyllosomas of Parribacus to be correct, although this cannot yet be shown with certainty. Sims' identification of his material was based in part on Saisho's personal communication, but Saisho (1966b)

apparently was not aware of Sims' 1965 paper when he reported 132 specimens of a phyllosoma designated *Parribacus* α and two specimens designated *Parribacus* β. These were collected in the Indian Ocean in connection with the International Indian Ocean Expedition, and are of the form attributed to *Parribacus* by Gurney. Saisho pointed out that the smaller specimens up to length 36.9 mm, designated *Parribacus* α (p. 218, fig. 16), appear to belong to the same species as Sims' "Phyllosome D." The two largest specimens, 47.2 mm (p. 219, fig. 17) and 64 mm (p. 220, fig. 18), have a relatively broader fore-body and were designated *Parribacus* β. Saisho suggested that *Parribacus* α might be a younger stage of *Parribacus* β, and if so, that a large β type should be found in Florida and adjacent Atlantic waters. This prediction is confirmed by the present record of the 65-mm larva from the Caribbean Sea, which appears quite similar to Saisho's largest specimen. It is clear that the fore-body of this species of phyllosoma, which is pear-shaped in early stages and only slightly wider than the hind-body, becomes progressively broader anteriorly and increasingly wider than the hind-body during the course of development.

A difficulty in accepting Gurney's identification, as Saisho (1966b) pointed out, was that the antenna in the first three stages of *Parribacus antarcticus* is biramous, the endopod having an articulation, whereas in later stages from the plankton believed by Gurney to belong to this

genus, the antenna up to TL nearly 35 mm is uniramous, without an outer process. In the specimen of 8.5 mm described herein, the antenna undoubtedly was biramous in earlier stages, but the exopod has been reduced to a small rounded process, which in the phyllosoma of 11.3 mm has disappeared entirely. There appears to be some sort of division near the distal end of both the left and right antennae in the 8.5-mm larva, but I am not certain whether this represents the remnant of the original articulation of the endopod, or is the result of damage to the specimen. In any case the condition of the antenna in this phyllosoma helps bridge the gap between the earliest stages of P. antarcticus described by Saisho and later stages from the plankton. In Sims' "Phyllosome D," 36.5 mm in length, the lateral process of the antenna is just beginning to become differentiated.

The absence of gill buds in the 65-mm phyllosoma described herein indicates that it does not represent the final phyllosoma stage of development. Prasad and Tampi (1965) mentioned four giant phyllosoma larvae collected in the Indian Ocean by the DANA Expedition. Three of these range in size from 76-80 mm and probably are final phyllosomas of P. antarcticus; the fourth, measuring 67 mm, according to the authors bears a close resemblance to the specimen from the Marshall Islands described by Johnson (1951).

I have examined the latter specimen, 70 mm in length (USNM 191794), and find it to resemble also the larva from

the Caribbean Sea, although it may belong to a different species; the fore-body differs somewhat in its proportions, having rather well defined anteriorly projecting "shoulders." In the collection of the USNM (257467) is a phyllosoma 63 mm in length taken 5 July 1963 at 16°00'N, 169°00'W, in the Pacific south of Johnston Island, roughly 1,000 km southwest of the Hawaiian Islands. This specimen agrees in all respects with the 65-mm phyllosoma from the Caribbean. The phyllosoma of 61 mm figured by Richters (1873: pl. 34, fig. 5) belongs in all probability to the same genus as the above-mentioned larvae, but almost certainly to a different species, having, as Johnson (1951) pointed out, a relatively broader hind-body. Richters' specimen of 75 mm (pl. 34, fig. 6) is undoubtedly a final phyllosoma and probably belongs to the same species as his 61-mm larva. Johnson mentioned that in the 75-mm phyllosoma the hind-body is broader than the fore-body; measurement of Richters' figure, however, shows the maximum width of the fore-body to be slightly greater than that of the hind-body. The phyllosomas 13 and 26 mm in length figured by Richters (pl. 34, figs. 2, 3) may be younger stages of the same species. His material was collected in south and east Asiatic waters and the South Seas. In the final phyllosoma of 75 mm the distal margins of the terminal article of the antenna as well as the outer margin of the lateral process are incised, suggesting the adult condition found both in *Parribacus* and *Arctides*, but not in *Scyllarides*. There is nothing to

indicate that these large phyllosomas are in any way abnormal in the sense of "giant larvae" discussed by Gurney (1942: 74-75).

The distribution of the phyllosomas discussed herein is consistent with the known geographic distribution of the adults of *Parribacus*. *P. antarcticus* occurs in the western Atlantic, where it does not seem to be very common, from Florida through the West Indies to Brazil, and is known throughout the Indo-West Pacific region to the Hawaiian Islands. Three other species of *Parribacus* were recognized from various Pacific localities by Holthuis (1960) as follows: *P. caledonicus* Holthuis, rather common on the reefs of New Caledonia; *P. scarlatinus* Holthuis from Kapingamarangi Atoll and the Marshall, Gilbert and Phoenix Islands; and *P. japonicus* Holthuis from Japan.

The possibility that these phyllosomas might belong to *Arctides* cannot be completely ruled out at this time, but in view of the apparent scarcity of adults of *Arctides* in the Indo-West Pacific region as well as for reasons discussed in the following section, I consider it unlikely.

H. ?Arctides guineensis (Spengler)

Materials and methods. I have examined more than 60 specimens ranging in length from about 6 to 59.2 mm. They were taken in plankton in the Atlantic off the coast of Florida and between the northern Bahama Islands and Bermuda. I tentatively refer these larvae to Arctides guineensis for reasons discussed herein. The collection data are given in Table 30. Complete station data are not available for several specimens collected by the GRAMPUS in 1914 (USNM 59586). Forty-two individuals of mean length 9.8 mm were collected at P-164. The subfinal stage is represented by three specimens. One was taken in the immediate vicinity of Bermuda (P-144). The largest phyllosoma is the final stage. Representative specimens are deposited in the Invertebrate Museum of this Institute (Acc. No. 32.3593).

Diagnosis of the Phyllosoma

Early stages with pear-shaped fore-body, biramous antenna, similar to Scyllarides and Parribacus. Pereiopod 5 becoming well developed at early stage, with setose exopod by TL about 10 mm. Eyestalk antennule ratio greater than in Scyllarides aequinoctialis, at TL 6-7 mm 1.55-1.8, at 7-8 mm 1.7-2.0. Fore-body by TL 6-7 mm slightly narrower

TABLE 30

LIST OF STATIONS AT WHICH PHYLLOSOMAS OF ?*ARCTIDES GUINEENSIS* WERE TAKEN

Station	Date (D/M/Y)	Position		Time	Gear	Gear depth(m)	Number of specimens	TL mm
		Lat. N	Long. W					
P-100	26/VII/64	30°06'	78°42'	2000-2100	1m plank. net	10-20	1	59.2
P-144	3/VIII/64	32°46'	64°33'	2025-2115	1m plank. net	10	1	49.5
P-160	6/VIII/64	29°27-28'	70°03-08'	2105-2203	1m plank. net	20	1	51.0
P-164	7/VIII/64	28°27-30'	73°39-42'	2115-2215	2m plank. net	2	42	5.8-19.4
P-165	7/VIII/64	28°25-27'	73°42'	2235-2335	1m plank. net	20-60	8	6.6-17.3
P-169	8/VIII/64	27°30'	76°27'	2115-2205	1m plank. net	sfc	1	8.5
P-190	10/VIII/64	27°25°	78°08'	2049-2225	2m plank. net	0-9	1	49.5
P-195	11/VIII/64	27°28'	78°19'	0345-0435	1m plank. net	20	1	13.0
P-196	11/VIII/64	27°37'	78°27'	0450-0545	1m plank. net	27	1	7.6
GRAMPUS 10163½	29/I/14	--	--	--	plank. net	0-400	1	20.8
GRAMPUS 10169c	1/II/14	--	--	--	"	sfc	1	20.3
GRAMPUS 10182	20/II/14	30°27'	66°05'	--	"	sfc	1	29.0
GRAMPUS 10188	24/II/14	--	--	--	"	0-30	1	32.3
GRAMPUS 10196	--/14	--	--	--	"	sfc	1	27.5
GRAMPUS 10209	--/14	--	--	--	"	sfc	2	25.0,29.3

than hind-body, becoming in subsequent stages torpedo-shaped and considerably narrower than latter. Length of final phyllosoma nearly 60 mm.

Characters of the Phyllosoma

The earliest phyllosomas of this form are undoubtedly similar to those of Scyllarides and Parribacus, having a biramous antenna and pear-shaped fore-body. It may not be possible to recognize diagnostic characters without laboratory reared material.

By TL 6-7 mm the fore-body is not quite as wide as the hind-body, about 1.7-1.8 times longer than wide, and narrow at the anterior end. Its posterolateral margins may cover the anterior part of the bases of maxilliped 3. In subsequent stages the fore-body remains elongated and becomes increasingly narrow in relation to the hind-body. Its outline comes to resemble that of a torpedo. In the final stage the fore-body is nearly twice as long as wide, with its maximum width at about 0.4 of its length from posterior to anterior, tapering gradually toward the anterior end. After TL about 12-14 mm the posterolateral margins no longer cover the bases of maxilliped 3.

The hind-body at TL 6-7 mm is slightly wider than the fore-body and in subsequent stages it becomes progressively broader relative to the latter. In intermediate stages the hind-body is 1.2 and in the last two stages about 1.4 times

wider than the fore-body. A posterior concavity in which the abdomen is situated forms in the hind-body as the rudiment of pereiopod 5 moves away from the base of the abdomen. In subsequent stages this concavity becomes quite wide and deep; the base of the abdomen in intermediate and late stages lies at a level anterior to the base of pereiopod 3. In these stages the maximum width of the hind-body, between the bases of pereiopod 3, is more than twice its length measured from the base of maxilliped 2 to the base of the abdomen.

The abdomen in early stages is more or less rectangular and narrow, probably with a short spine and a few small setae at each posterolateral angle, which soon disappear. After TL 9-10 mm the abdomen no longer extends to the level of the base of pereiopod 5 until the last two stages, when it becomes well developed. In the final stage the abdomen extends well beyond the posterior margin of the hind-body. The segments are marked off most clearly dorsally near the midline. Segments 2-5 have a short, blunt spine or tubercle on each side at the posteroventral margin. The posterodorsal margin at the midline of segment 4 is not projected, while segment 5 has only a slight, broad-based triangular projection, not in the form of a definite spine or tubercle as found on segments 4-5 in the final phyllosoma of Scyllarides spp. The telson is without spines. In later stages its posterior margin becomes rounded.

As in other phyllosoma larvae, the eye probably becomes

stalked at the first ecdysis. At this stage the eyestalk is probably shorter than the antennule, but in subsequent stages the eyestalk becomes increasingly longer relative to the latter. At TL about 6-8 mm, before other differences become marked, I find the eyestalk/antennule ratio to be a character useful in separating the phyllosomas of this species from Scyllarides aequinoctialis. At TL about 6 mm the eyestalk is 1.55-1.70 times longer than the antennule, at 7 mm 1.7-1.9, and by TL 8 mm the eyestalk is about twice the length of the antennule. In intermediate and late stages the ratio is nearly 3, and in the final stage about 2.7.

Maxilla 1 is biramous, without palp. The coxal endite in early stages has one stout, elongated terminal seta plus a similar but smaller seta and a few terminal and subterminal spines or setae; the basal endite has two strong terminal teeth and a few spines or setae. At TL about 8-9 mm a third terminal tooth appears on the basal endite; in the final stage the basal endite of one side may bear four terminal teeth. The second terminal seta of the coxal endite becomes as large as the other. Spines or setae are added to both endites as development progresses.

Maxilla 2 in early stages consists of a basal segment and a smaller, narrow apical article bearing four long, plumose setae. These setae begin to be lost between TL 6-8 mm. In most individuals over TL 8 mm the apical segment is without setae and not distinctly marked off from

the basal portion. The anterior margin of the latter has a small seta distally. In late stages the distal portion expands and becomes broader than the basal portion. In the final stage it assumes the paddle-shaped form of the scaphognathite.

The antennule is no doubt unsegmented in the earliest stages. By TL 6 mm the inner flagellum is differentiated as a short bud, the outer flagellum is marked off from the peduncular portion, and the latter consists of two segments. At TL 12-13 mm a third segment appears in the antennular peduncle. Aesthetascs are added in tufts along the medial side of the outer flagellum and the inner flagellum increases gradually in length as development progresses. In the final stage the distal article of the antennular peduncle is somewhat shorter than the proximal two. The inner flagellum is slightly shorter than the outer flagellum.

The antenna in early stages is biramous. The branches are not articulated with each other, but the basal portion of the endopod is articulated with a cylindrical apical segment bearing a few small terminal setae. By TL 6 mm the antenna, which in the first stage is probably not much shorter than the antennule, has become quite short, and the exopod is reduced to a small triangular process. At TL about 14-15 mm an articulation marks off the base of the endopod from the basal portion of the antenna. The exopod is a much reduced process at the outer distal end of the latter. The antenna in subsequent stages gradually increases

in length and becomes divided into five more or less distinct segments, including the basal portion. The exopod is reduced to a minute toothlike projection at TL 25 mm, and disappears entirely by TL 29 mm. At this length the incipient lateral process is indicated as a slight swelling at the outer distal end of the second article. In subsequent stages it becomes a prominent triangular process. In the final stage the antenna is slightly longer than the antennule. The lateral process is broad; its margins as well as those of the terminal article are entire.

Maxilliped 1 is first indicated at TL about 16 mm as a slight elevation posterior to the base of maxilla 2. In subsequent stages is becomes a conical bud, which in the subfinal stage shows indications of differentiation. In the final stage maxilliped 1 is a finger-like process, with a posteriorly directed lobe laterally representing the epipodite.

Maxillipeds 2 and 3 each consist of five segments and in the early stages lack an exopod, although the second segment of maxilliped 3 has on its outer side a slight bump representing the presumptive exopod bud. The distal portion of the propodus of both maxillipeds is provided with spines or setae which increase in number as development progresses. The dactyl of maxilliped 3 is similarly armed. In the subfinal stage both maxillipeds have a small, rounded exopod bud, which in the final stage becomes a short, oval bud without setae. The coxal segment of maxilliped 2 in the

final stage has an epipodite attached at the outer distal end.

The early development of the pereiopods probably parallels that of Scyllarides aequinoctialis and Parribacus. Pereiopod 5 becomes well developed at a relatively early stage. By TL 6 mm pereiopods 1-4 are well developed and possess setose exopods, while pereiopod 5 is an elongated bud 1-1.5 times the length of the abdomen, with the exopod already indicated as a minute bud. From TL about 7-9 mm pereiopod 5 is an elongated rudiment 3-9 times the length of the abdomen, with the coxal segment clearly demarcated and the rest of the appendage showing some segmentation. The exopod is an elongated rudiment without setae. By TL about 10 mm the exopod in most individuals has acquired natatory setae, and by TL 16 mm the basis of pereiopod 5 is nearly as long as that of pereiopod 4. The pereiopods, which on one side of the final phyllosoma are all intact, present some interesting features. The lengths of the various segments are given in Table 31. Pereiopods 1 and 2 are relatively short and slender; the distal portion of the propodus is provided with numerous spines or setae, and the dactyl is short and claw-like, that of pereiopod 2 being slightly the longer. Pereiopods 3-5 are longer and more robust than the first two. Pereiopod 3 has a much elongated blade-like dactyl. Pereiopods 4-5 are similar to each other, differing only slightly in the length of the various segments. The propodus is much elongated, about 1.4 times the

length of that of pereiopod 3, but the dactyl is short, extending only slightly beyond the dilated end of the propodus. The latter lacks spines or setae.

Pereiopods 1-3 have a coxal spine in early stages. By TL 6 mm the spines are short and inconspicuous, and by TL 8 mm they have more or less entirely disappeared. No coxal spines are present in later stages.

The number of pairs of natatory setae on the exopods of pereiopods 1-2 in stage I is unknown. There are probably five or six. The number may increase by one pair per molt in the first few stages, but in intermediate and late stages apparently more than one pair may be added at an ecdysis. The exopods of pereiopods 1-5 in the final stage bear respectively 38, 36, 38, 37½ and 36 pairs of setae. The number in various stages is given in Table 32.

The uropods are first visible at TL 16-19 mm as low folds in the cuticle, which at TL 25 mm appear as small, shallowly bilobed buds. They increase in size in subsequent stages and in the subfinal stage are well developed. The outer ramus, articulated at the base, is slightly longer than the inner and extends beyond the posterior margin of the telson. In the final stage both rami project somewhat beyond the latter.

The pleopods, especially the first two pairs, are indicated at TL 25 mm as low, crescent-shaped folds in the cuticle. In the subfinal stage they are biramous. The pleopods in the final stage are elongated and leaf-like;

the endopod is slightly longer than the exopod and there are indications of articulation to the protopodite. The appendix interna is indicated in the subfinal stage as a swelling on the medial side of the endopod, and in the final stage it appears as a short cylindrical process.

Small, slender gill buds are present only in the final stage. Their distribution corresponds to that of Scyllarides.

Description of Illustrated Stages

Length 6.6 mm (fig. 99). P-165. Fore-body pear-shaped, narrow at anterior end, 1.7-1.8 times longer than wide; posterolateral margins just or not quite covering anterior end of base of maxilliped 3. Hind-body slightly wider than fore-body. Abdomen situated in shallow concavity of hind-body, short, narrow, without spines, uropods or pleopods, extending beyond level of base of pereiopod 5. Eyestalk about 1.8 times length of antennule. Outer antennular flagellum marked off from peduncular portion; inner flagellum a short bud; peduncle with two segments, proximal twice length of distal. Antenna biramous, short; rami not articulated with each other; basal portion of endopod articulated with small cylindrical apical segment; latter with two or three small terminal setae; exopod a short pointed process. Maxilla 1 biramous, without palp; coxal endite with one stout, elongated terminal seta plus a somewhat smaller but similar seta and a few slender spines or setae; basal endite

with two strong terminal teeth. Maxilla 2 consisting of basal segment and smaller, narrow apical article, latter with two or three long, plumose terminal setae; anterior margin of basal segment with a small seta distally. Maxilliped 1 not indicated. Maxillipeds 2 and 3 each with five segments, without exopod; second segment of maxilliped 3 with slight bump laterally representing presumptive exopod bud. Pereiopods 1-4 well developed, with setose exopod. Pereiopod 5 an elongated bud about 1.5 times length of abdomen, and removed from base of latter; exopod indicated as minute bud. Pereiopods 1-3 with short, inconspicuous remnant of coxal spine.

Length 8.6 mm (fig. 100). P-164. Proportions of fore-body not much changed. Hind-body about 1.06 times wider than fore-body, with maximum width between bases of pereiopod 2; posterior concavity deeper; abdomen extending slightly beyond level of base of pereiopod 5. Eyestalk more than twice length of antennule. Antennular peduncle still with two segments. Outer ramus of antenna extending about to articulation in inner ramus. Basal endite of left maxilla 1 with two terminal teeth, that of right side with three. Apical segment of maxilla 2 without terminal setae, not distinctly marked off from basal portion. Pereiopod 5 an elongated rudiment more than 4.5 times length of abdomen, with coxal segment clearly demarcated; rest of appendage showing incomplete division; exopod an elongated rudiment without setae. No coxal spines present.

Length 11.6 mm (fig. 101). P-164. Fore-body nearly 1.8 times longer than wide, with posterolateral margins not quite covering base of maxilliped 3. Hind-body about 1.1 times wider than fore-body, deeply concave behind. Abdomen not extending to level of base of pereiopod 5. Eyestalk nearly 2.3 times length of antennule. Antennular peduncle with indications of a third segment. Basal endite of maxilla 1 with three terminal teeth. Pereiopod 5 smaller than pereiopods 1-4, but possessing a functional exopod bearing 7½ pairs of natatory setae.

Length 16.6 mm (fig. 102). P-164. Fore-body pear-shaped, narrow, about 1.8 times longer than wide, tapering gradually toward anterior end. Hind-body broad, about 1.2 times wider than fore-body, deeply concave behind; maximum width more than twice the length measured from base of maxilliped 2 to base of abdomen. Latter narrow, little developed. Eyestalk about 2.7 times length of antennule. Antenna not extending to end of first article of antennular peduncle; an articulation between base of endopod and basal portion; exopod a short process at outer distal end of latter; second article of antenna longer than before, with traces of an additional articulation. Maxilliped 1 indicated as faint elevation posterior to base of maxilla 2. Pereiopod 5 with basis nearly as long as that of pereiopod 4; basis of both pereiopods somewhat longer than that of pereiopods 1-3. Exopod of pereiopod 5 with 16 pairs of natatory setae.

Length 29.0 mm (fig. 103). GRAMPUS 10182 (USNM 59586). Fore-body 1.8 times longer than wide, with posterolateral margins not covering bases of maxilliped 3. Hind-body slightly more than 1.2 times wider than fore-body, with maximum width between bases of pereiopod 3. Eyestalk nearly three times length of antennule. Segments of antennular peduncle subequal in length. Antenna extending slightly beyond end of second article of antennular peduncle, with five more or less clearly differentiated segments, including basal portion; no trace of exopod; incipient lateral process indicated as slight swelling at outer distal end of second article. Maxilliped 1 a conical bud. Uropods small, bilobed buds. Pleopods indicated as low, crescent-shaped folds in cuticle.

Length 49.5 mm (fig. 104). Subfinal stage. P-190. Fore-body narrow, torpedo-shaped, nearly 1.8 times longer than wide. Hind-body quite broad, nearly 1.4 times wider than fore-body; posterior concavity wide and deep; base of abdomen lying at level anterior to base of pereiopod 3. Abdomen well developed, extending slightly beyond level of base of pereiopod 5; segmentation clearest dorsally near midline. Segments 2-4 with a short, obtuse tubercle on each side at posteroventral margin. Telson without spines, posterior margin rounded. Eyestalk nearly three times length of antennule. Antenna extending about to middle of outer antennular flagellum, with five more or less distinct segments; outer distal portion of second article with

prominent triangular process. Distal portion of maxilla 2 somewhat expanded, broader than basal portion. Maxilliped 1 a bud showing indications of differentiation. Second segment of maxillipeds 2 and 3 with a small, rounded exopod bud. Uropods well developed; outer ramus slightly longer than inner, articulated at base, extending beyond posterior margin of telson. Pleopods biramous; incipient appendix interna indicated as swelling on medial side of endopod. No gill buds present.

Length 59.2 mm (fig. 105). Final stage. P-100. Fore-body narrow, torpedo-shaped; length about twice the width; maximum width at about 0.4 of length from posterior to anterior, tapering gradually toward anterior end; postero-lateral margins not covering base of maxilliped 3. Hind-body broad, about 1.4 times wider than fore-body; posterior concavity deep; base of abdomen lying at level anterior to base of pereiopod 3. Abdomen nearly as long as hind-body measured from base of abdomen to base of maxilliped 2, extending well beyond level of base of pereiopod 5; segments more or less clearly marked off dorsally; segments 2-5 with a short, blunt spine or tubercle on each side at postero-ventral margin. Posterodorsal margin at midline of segment 4 not projected; segment 5 with only a low, broad-based triangular projection, not in form of a definite spine or tubercle. Telson without spines. Eyestalk about 2.7 times length of antennule. Distal article of antennular peduncle slightly shorter than proximal two; inner flagellum slightly

shorter than outer flagellum. Antenna slightly longer than antennule, with five more or less distinct segments; second article with broad, expanded lateral process; margins of latter and terminal article of antenna entire. Coxal endite of maxilla 1 with two stout, elongated terminal setae plus several smaller terminal and subterminal spines or setae; basal endite of left maxilla 1 with three strong terminal teeth plus a few smaller spines or setae, that of right side with four terminal teeth. Distal portion of maxilla 2, representing exopod, expanded in paddle-shaped form of scaphognathite. Maxilliped 1 a finger-like process, with a posteriorly directed lobe near base representing epipodite. Second segment of maxillipeds 2 and 3 with a short, oval exopod bud without setae. Coxal segment of maxilliped 2 with epipodite at outer distal end. Pereiopods 1 and 2 relatively short and slender; distal portion of propodus provided with numerous spines or setae; dactyl short, claw-like, that of pereiopod 2 slightly the longer. Pereiopods 3-5 longer and more robust. Dactyl of pereiopod 3 much elongated, blade-like. Pereiopods 4-5 similar to each other; propodus much elongated, about 1.4 times length of that of pereiopod 3, slightly expanded at distal end, without spines or setae. Dactyl of pereiopods 4-5 short, extending only slightly beyond inner distal angle of propodus. Exopods of pereiopods 1-5 respectively with 38, 36, 38, 37½ and 36 pairs of natatory setae. Uropods well developed, both rami extending beyond end of telson; outer ramus, articulated at

TABLE 31

LENGTH IN MM OF THE VARIOUS SEGMENTS OF THE PEREIOPODS IN THE FINAL PHYLLOSOMA (TL 59.2 MM) OF ?*ARCTIDES GUINEENSIS*

Pereiopod	Coxa	Basis	Ischiomerus	Carpus	Propodus	Dactyl
1	4.7	20.6	7.0	6.6	27.8	1.7
2	5.2	19.8	9.7	8.2	34.7	2.4
3	5.3	16.5	21.9	19.4	43.6	10.0
4	5.6	23.0	23.8	21.0	60.0	2.0
5	6.0	26.1	22.5	20.8	62.8	1.8

TABLE 32

NUMBER OF PAIRS OF NATATORY SETAE ON THE EXOPODS OF PEREIOPODS 1-5 IN VARIOUS PHYLLOSOMA STAGES OF ?*ARCTIDES GUINEENSIS*

TL (mm)	P. 1	P. 2	P. 3	P. 4	P. 5
5.8	11	11	9	6	
6.6	12	12	10	8	
7.2	12	13	10	8	
7.8	13	13	12	10	ex.rud.
8.4	14	14	12	10	ex.rud.
9.2	15	15	13½	12	0
9.7	15	15	13	12	0,4½
9.8	15	15	13	11½	0
10.7	15	16	14	13	4½
10.9	15	16	14	13	6
11.6	16	16	14½	13	7½
13.6	17½	18	16	16	11½
15.0	19	19	18	17	13½
16.6	20½	21	19	18½	16
19.4	21	22	21	20	17
29.0	29½	29	28	27	26
49.5	36	36	36	35	34
59.2	38	36	38	37½	36

base, slightly longer than inner. Pleopods elongated, leaf-like, with indications of articulation to protopodite; endopod slightly longer than exopod, with small cylindrical process medially representing appendix interna. Small, slender gill buds present.

Discussion. This form of phyllosoma, the features of which are quite distinctive after the early stages, is apparently one of the most infrequently reported in the literature. The only previous accounts of which I am aware are by Bate (1888) and Verrill (1922). Bate described and illustrated (pl. 12C, fig. 1) a phyllosoma 30 mm in length taken by the CHALLENGER off St. Thomas in the West Indies. He mistakenly believed it to be the larva of a species of Panulirus. Bate mentioned the resemblance of this specimen to the Phyllosoma stylicornis of Milne-Edwards (1837, pl. 28, figs. 1-7) from the Indian Ocean, but pointed out the difference between the two in the proportions of the fore-body. Gurney (1936) suggested that the larva reported by Bate might belong to the same species as the phyllosoma from the equatorial Atlantic which Gurney tentatively designated Parribacus sp? (p. 438, fig. 42). Both Gurney's larva and the specimen figured by Milne-Edwards appear to belong to the form dealt with in the present work under Parribacus. Bate's specimen, having the characteristic narrow, elongated fore-body and broad hind-body, undoubtedly belongs to the same species as the phyllosomas described herein. Verrill recognized that the species of phyllosoma

described by Bate was distinct from Panulirus and speculated that it "may belong to Scyllarus or one of the species of Scyllarides, but its origin is very uncertain." It is not quite clear from his account whether Verrill had taken specimens of this phyllosoma in the Gulf Stream and adjacent waters around Bermuda, as he had phyllosomas of Panulirus, or whether he was referring only to the specimen reported by Bate. The figure given by Verrill (pl. 3A, fig. 4) is a reproduction of Bate's.

If my identifications of the phyllosomas of Scyllarides and Parribacus are correct, it seems likely that this phyllosoma belongs to Arctides guineensis. Species of the genus were formerly placed in Scyllarides, which is closely related (Holthuis, 1960). The development of the phyllosoma parallels that of Scyllarides aequinoctialis. It differs from the latter chiefly in the proportions of the fore- and hind-body and the eyestalk, the form of the dactyl of pereiopod 4, and the absence of a spiniform process at the postero-dorsal margin in the midline of abdominal segments 4-5 in the last stages, in addition to the greater ultimate size attained. The pattern of development of the antenna is similar to both species of Scyllarides dealt with herein, and differs from the form attributed to Parribacus. Although in the adult of Arctides the distal antennal article differs from that of Scyllarides in bearing a number of distinct teeth, it is entire in the final phyllosoma described herein, as in the final phyllosomas of the two species of

Scyllarides.

According to Verrill (1922), adults of Arctides guineensis (reported as Scyllarides sculptus bermudensis) seemed to be rare at Bermuda, but were taken in lobster pots off the outer reefs. The geographic distribution of the phyllosomas here referred to Arctides is consistent with that of the adult, which in the western Atlantic is known primarily from Bermuda and the Bahamas. The relative abundance of the phyllosomas in the waters between these localities suggests that adults of Arctides may be more common, perhaps in less accessible reef areas, than existing records would indicate. The species probably occurs also in the West Indies. Although Holthuis (1963) remarked that Arctides seemed to be very rare at New South Wales, and has only recently been found in the Indian Ocean (Holthuis, personal communication), it seems rather surprising that phyllosomas of this form have never been recorded from the Indo-West Pacific region. Arctides regalis Holthuis, which closely resembles the Atlantic species (Holthuis, 1963), seems to be fairly common in Hawaiian waters (Holthuis and Mr. Lester Zukeran, personal communication).

The distribution of the phyllosomas reported herein shows no seasonal pattern. The final and subfinal stages as well as a number of relatively early stages were collected in July and August. Intermediate stages were taken by the GRAMPUS in late January and February.

I. Phyllosoma Q

(Figure 110)

Material. This phyllosoma is represented by a single specimen 10.8 mm in length, collected on 21 Aug. 1962 at G-47 in the Straits of Florida off Miami (25°39'N, 79°40'W). It was taken at 1906-1935 hours in a 6' IKMT at a depth of approximately 162 meters. The larva is deposited in the Invertebrate Museum of this Institute (Acc. No. 32.3594).

Description

Fore-body pear-shaped, 1.4 times longer than wide, 1.25 times wider than hind-body, tapering gradually anteriorly; width at anterior end between bases of antenna nearly 1/3 maximum width; posterolateral margins just covering base of maxilliped 3. Maximum width of hind-body, between bases of pereiopod 2, about 1.15 times length of hind-body measured from bud of maxilliped 1 to base of abdomen. Latter short, little more than 1/5 length of hind-body, broad at base, tapering posteriorly, forming a continuation of hind-body from bases of pereiopod 5. Telson short, without spines; margins more or less rounded, with slight indentation at midline. Eyestalk long, slender, 1.4 times length of antennule. Antennular peduncle with three distinct segments,

ratio of lengths from proximal to distal 100:73:61. Inner flagellum slightly more than half length of outer flagellum; medial margin of latter provided with numerous aesthetascs. Antenna slightly less than half length of antennule, extending beyond end of first article of antennular peduncle and somewhat broader at base than latter, tapering distally; a very small triangular lateral process near middle of its length; an articulation indicated distal to process; no other division apparent. Maxilla 1 biramous, without palp; coxal endite with one stout, elongated terminal seta plus four smaller terminal and two subterminal spines; basal endite with three strong terminal teeth plus a few small spines or setae. Maxilla 2 a single segment without setae; distal portion not quite as broad as basal portion, but beginning to expand. Maxilliped 1 a distinct, low rounded bud posterior to base of maxilla 2. Maxillipeds 2 and 3 each with five segments, without exopod; second segment of maxilliped 3 with a small bump on outer side representing presumptive exopod bud. Pereiopods 1-5 well developed, with functional exopods; endopods broken off at basis-ischiomerus joint; basis of pereiopod 5 somewhat shorter than that of pereiopod 4; exopods respectively with 15, 16, 14, 12 and 9 pairs of natatory setae. Maxilliped 3 and pereiopods 1-4 with a small, inconspicuous coxal spine; pereiopod 5 without coxal spine. Uropods short, biramous rudiments; outer ramus oval, longer than inner ramus, not extending to posterior margin of telson. Pleopods four pairs of low, undifferentiated

buds.

Discussion. This unique phyllosoma possesses a remarkable combination of characters. The form of the abdomen is characteristic of all known phyllosomas of *Scyllarus* at a similar stage, and is unknown in any other genus. On the other hand, a well developed pereiopod 5, with setose exopod, is unknown in any larva of *Scyllarus*. The form of the antenna and of maxilla 2 resembles *Scyllarus*, while the shape and proportions of the fore-body and the length of the eyestalk are similar to the *Scyllarides* type of phyllosoma. The phylogenetic implications are pointed out in the General Discussion section.

There is a possibility that this specimen may belong to *Scyllarus faxoni*, the only western Atlantic species of *Scyllarus* the larvae of which I have been unable to account for in the present investigation. The phyllosoma is so atypical, however, that I am reluctant to assign it to any known species of Scyllaridae without additional evidence. I have therefore designated it "Phyllosoma Q" to call attention to its uncertain identity. The possibility that it may belong to an undiscovered scyllarid lobster must be considered. Gurney (1942) pointed out:

> Since the larvae are easily taken in plankton, whereas the adults may live in places where they cannot be reached by trawl or dredge, it is not surprising that we already know many larval forms which belong to genera as yet undiscovered. This is probably true of Phyllosoma. . . .

PART V

GENERAL DISCUSSION

Larval characters of Scyllarus. Gurney (1936) in his study of the phyllosoma larvae collected by the DISCOVERY found "strong evidence that, within the genus Scyllarus, specific differences in the larvae are very small or non-existent." Obviously one of the chief reasons that Gurney was unable to recognize differences was the erroneous identification as Scyllarides of phyllosomas of certain species of Scyllarus. The lack of complete developmental sequences and in some instances the probable inclusion in a single sequence of larvae belonging to more than one species contributed to the difficulty.

More recent reports dealing with larvae of Scyllarus (Prasad and Tampi, 1957, 1960a, b; Al-Kholy, 1960; Baisre, 1964, 1966; Sims, 1966b; Saisho, 1964b, 1966b), as well as the results of the present investigation, indicate that certain differences do exist among the larvae of many species of the genus. Some are easily recognized; others are a matter of detail. Among the morphological features having diagnostic value at various stages of development are chromatophore distribution, total length, the shape and proportions of the fore-body and its width relative to the

hind-body, the number of pairs of natatory setae on the exopods, the relative lengths of the eye and stalk and first and second antennae, the length of the medial spine or seta of the antennule, the number of apical setae of maxilla 2, the presence or absence of conspicuous dorsal spines at the edge of the hind-body adjacent to the insertion of the pereiopods, the length of the posterolateral telson spines and the shape of the uropods.

The length of the first phyllosoma among those species for which information is available ranges from 1.05 mm (*S. bicuspidatus*, Saisho, 1964b; *S. sordidus*, Prasad and Tampi, 1960) to a maximum of 1.7 mm for *S. americanus*. The final phyllosoma ranges from about 9 mm for various species to 28 mm reported for *S. arctus* by Stephensen (1923). The length of the final phyllosoma appears to be independent of the ultimate size attained by the adult of the species.

Most later phyllosomas of *Scyllarus* fall into one of two groups by the outline of the fore-body: (1) those with a more or less rounded or subcircular fore-body; and (2) those with a subquadrate or trapezoidal fore-body. The telson spines attain a maximum development in the phyllosomas from the eastern Atlantic and Mediterranean belonging probably to *S. pygmaeus*, and are only slightly shorter in *S. arctus* and *S. nearctus*. In the 9.5 mm larva designated "*Scyllarides* sp." by Prasad and Tampi (1960: 248, fig. 11) the telson is devoid of spines. The telson spines of most species are intermediate between these extremes. Prasad

and Tampi's specimen differs also from most other species of *Scyllarus* in having two small but distinct serrations on the lateral process of the antenna. The uropods in larvae of most species are rounded or oval in outline, whereas they are characteristically pointed in certain forms from the Indo-West Pacific region attributed by previous investigators to *Scyllarides*.

The number of pairs of natatory setae on the exopod of pereiopods 1-2 is a useful diagnostic character in the first two or three stages before more conspicuous differences become apparent. In a given species the number on pereiopod 2 appears to be slightly less variable than on pereiopod 1. The number of pairs in stage I ranges from five (*S. bicuspidatus*, Saisho, 1964b; *S. arctus*, Hornell, 1894 (fig.); *S. nearctus*) to eight in *S. americanus*.

The number of plumose apical setae on maxilla 2 is in certain instances a useful character in early stages, but it varies in some species and must be used with discretion. Four seems to be the most frequent number in the majority of species, but some individuals may possess only three. Larvae of *S. americanus* appear always to have three setae. In occasional specimens of *Scyllarus* n. sp. there are five.

The antennule in stage I of most species bears a small spine or seta medially somewhat beyond the middle of its length. In *S. nearctus* and apparently *S. arctus* there is a relatively prominent spine. Among western Atlantic species, the dorsal spines at the edge of the hind-body adjacent to

the insertion of pereiopods 1-4 are characteristic of later stages of *S. nearctus*. They are present also in similar phyllosomas (USNM) collected by the ALBATROSS Philippines Expedition, but are not mentioned in accounts of *S. arctus*. The antenna in intermediate and later stages of *S. nearctus* is relatively longer than in other western Atlantic species. A characteristic chromatophore is located on each side of the fore-body in stage I of *S. nearctus*.

Gurney's definition of the generic larval characters of *Scyllarus*, founded on *S. arctus*, may be provisionally updated to include new information as follows: Fore-body much wider than hind-body; subcircular, subquadrate or trapezoidal in outline. Hind-body not concave posteriorly. Abdomen in later stages broad at base, forming direct, tapering continuation of hind-body. Antenna in early stages uniramous, much shorter than antennule; in later stages broad, with prominent lateral process; flagellum short, broad, margins not distinctly serrated. Maxilla 1 without palp. Maxilla 2 in early stages with 3-5 apical setae, in later stages without setae. Maxilliped 2 with small exopod bud only in last stages. Maxilliped 3 without exopod. Pereiopod 3 in stage I not much longer than pereiopod 2. Pereiopod 4 in stage I only a minute bud at base of abdomen. Pereiopod 5 (present after early stages) rudimentary, without exopod. All pereiopods with a coxal spine and a short claw-like dactyl. Pleopods in final stage biramous, narrow; appendix interna only indicated, not a free process.

Uropods rounded, oval or pointed. Telson with long, short or no posterolateral spines. Gill buds present only in final stage; maxilliped 2 without epipodite.

Larval characters of Scyllarides. The generic larval characters of Scyllarides, based on the present investigation, are provisionally as follows: Fore-body in early stages pear-shaped, later oval or subelliptical in outline, longer than wide and somewhat wider than hind-body. Abdomen after early stages situated in posterior concavity of hind-body; in last stages with a spiniform process dorsally at posterior midline of segments 4 and 5. Antenna in stage I biramous, somewhat shorter than antennule; exopod becoming progressively smaller but persisting until lateral process becomes differentiated. Antenna in late stages broad, with prominent lateral process; flagellum short, broad, margins entire. Maxilla 1 without palp. Maxilla 2 with four apical setae in early stages, without setae in subsequent stages. Maxillipeds 2 and 3 with small exopod bud only in last stages. Pereiopod 3 in stage I about 1.3 times length of pereiopod 2; dactyl of pereiopod 3 after early stages much elongated, blade-like. Pereiopod 5 in some species becoming well developed, with setose exopod, at relatively early stage; in others remaining rudimentary throughout development. Pereiopods after early stages without coxal spines. Telson after early stages without spines. Pleopods in final stage deeply biramous, leaf-like; appendix interna a short, free process. Gill buds present only in

final stage; maxilliped 2 with epipodite. Length of final stage from 36 to 51 mm.

Systematic characters of pereiopods. Gurney (1936) observed that the legs of phyllosomas sometimes "present striking features which would be useful systematically if available generally for comparison." This is true of the later stages of *Scyllarides*, *Parribacus* and ?*Arctides*. Unfortunately the endopods of specimens collected in the plankton are often broken off at the basis-ischiomerus joint. Pereiopods 1 and 2 in each of the above forms are relatively short and slender, with short dactyls. The much elongated, blade-like dactyl of pereiopod 3 may have an important function in the feeding behavior of the larva. There are interesting differences among genera in the dactyls of pereiopods 4 and 5. The dactyl of pereiopod 4 has its maximum development in the specimen of 70 mm belonging probably to *Parribacus* (reported by Johnson, 1951), being as long as the dactyl of pereiopod 3. In *Scyllarides aequinoctialis* the dactyl of pereiopod 4 is not quite half as long as that of pereiopod 3, and resembles the dactyl of pereiopod 5 of *Parribacus*. The dactyl of pereiopod 5 in *S. aequinoctialis* is short and similar to that of pereiopod 4 of *Scyllarides nodifer* and pereiopods 4 and 5 of ?*Arctides*. Whereas in *Parribacus* the dactyl of pereiopod 4 is long and resembles that of pereiopod 3, in *Arctides* it is short and essentially identical with the dactyl of pereiopod 5.

In phyllosomas of Scyllarus the basis is fused to a greater degree with the ischiomerus and the legs are seldom lost. They show few features of systematic interest, however, the dactyls of all pereiopods being relatively short and claw-like.

Phylogenetic aspects. The precise origins of the Scyllaridea, as in the case of most major decapod groups, are obscure. They are generally thought to be an offshoot of the extinct Triassic Pemphicidea (Glaessner, 1960) or Glypheidea (Burkenroad, 1963). The Family Palinuridae first appears in the Jurassic, the Scyllaridae in the Cretaceous. The fossil genus Cancrinus Munster, 1839, from the Liassic of Europe is regarded as transitional between the palinurids and scyllarids because of its peculiar antenna (Boas, 1880; George and Main, 1967).

The latter authors have treated extensively the phylogenetic relationships of the Palinuridae. Recent investigators have had little to say concerning the affinities of the Scyllaridae, although the problem has been discussed by Boas (1880) and by Bouvier (1917, 1940). Glaessner (1960) observed that "There is still some doubt about homologies and evolution in the Scyllaridea. . . . "

Boas (1880) in his valuable work on decapods showed that the scyllarids resemble in a number of characters the more primitive palinurids, especially Jasus lalandii. He concluded (p. 90) that the scyllarids were derived from a form closely related to the latter. A similar view was

expressed by Bouvier (1917: 103): "Il faut donc chercher dans les Palinurides très primitifs, issus vraisemblablement des Glyphéidés, origine des Scyllaridés." Bouvier attributed the characteristic form of the presumably more primitive scyllarids to the neotenous persistence of an adaptive form of the postlarval stage:

> Et dès lors, la carapace aplatie et carénée de beaucoup des Scyllaridés adults nous apparaît, non comme un produit d'atavisme indiquant une parenté avec des types plus anciens, mais comme la persistance d'une forme adaptative propre au stade natant de cette famille.

George and Main (1967) did not consider larval characters. The phyllosoma larvae of the Scyllaridea are so highly specialized that, as Gurney (1942) remarked, they "cannot easily be compared with any other." Seebach (1873) identified as phyllosoma larvae certain arthropod-like fossils from the Solenhofen limestone of Jurassic age. His figures show little of comparative value, although he mentioned that in many specimens the ten legs were fully developed and the fifth pair was fully as large as the fourth. It is not within the scope of the present work to examine all evidence relating to the phylogenetic affinities of the Scyllaridae, but a comparison of the various forms of recent phyllosomas may provide additional evidence of relationships between and within the Palinuridae and Scyllaridae.

The genus Palinurellus is a logical point of departure because of its undoubted primitiveness. It has been the

general practice for a number of years to regard this peculiar decapod as the most primitive living representative of the Palinuridae. George and Main (1967), however, have recently agreed with Bate (1881) and de Man (1881, 1882) that Palinurellus, which "has obvious affinities with the Scyllaridae and Polychelidae as well as with the Palinuridae," should be removed from the latter and placed in a separate family, the Synaxidae.

A sequence of larval stages belonging with probability to Palinurellus gundlachi von Martens, 1878 has recently been described by Sims (1966b) from planktonic specimens collected in the western Atlantic. Larvae presumably of this genus were formerly known by the generic name "Phyllamphion." The presence of a prominent triangular rostrum is a unique feature characteristic also of the adult. Later stages differ from typical phyllosomas in that the quadrate fore-body extends over most of the thorax, a superficial resemblance to the form known as "Amphion" (see Gurney, 1936). A similar condition is found in the peculiar palinurid phyllosoma belonging possibly to Puerulus, a primitive genus. The circular cephalic shield in a specimen 17 mm in length extends posteriorly to cover more than half the abdomen (see Saisho, 1966b: 213, fig. 13). In the majority of phyllosomas gill buds appear at the ecdysis to the final phyllosoma stage; an atypical feature of Palinurellus is the progressive appearance of gill buds beginning, with the anterior podobranchia,

several stages before the final phyllosoma. Pereiopod 5 becomes well developed, with a setose exopod, at a relatively early stage. The antennal flagellum in the final phyllosoma is not markedly elongated.

The first stage of Palinurellus as described by Sims is a fairly typical palinurid phyllosoma, having a setose exopod on maxilliped 3. The antenna is biramous; according to Sims the endopod has an articulation and is slightly longer than the exopod. The first phyllosoma does not appear to differ a great deal from the stage I phyllosoma of Panulirus, regarded as the most highly evolved palinurid genus, except that the antenna in the latter is uniramous. Prasad and Tampi (1959: 161-162, fig. 17) have assigned to Panulirus sp. three stage I phyllosomas with a biramous antenna, collected in plankton in the western Indian Ocean. They felt that since Feliciano (1956) had shown the presence of a biramous antenna in the so-called prenaupliosoma stage of Panulirus argus, the possibility that it might persist in the first phyllosoma of some species of Panulirus "cannot be completely ruled out." Their specimens differ from all known stage I larvae of Panulirus (see Saisho, 1964a) in certain other features, including the possession of short, claw-like dactyls on all three pereiopods, a larger number of pairs of natatory setae on the exopods, and five rather than four apical setae on maxilla 2. The first stage presumably of Palinurellus gundlachi agrees in all these characters with Prasad and Tampi's specimens. The

latter apparently differ from *Palinurellus gundlachi* in that the endopod of the antenna lacks an articulation, and no rostrum is mentioned. I consider it probable that these larvae belong to one of the more primitive palinurids such as *Puerulus* or *Palinurellus wieneckii* (de Man), both known from the area where the phyllosomas were collected (see Holthuis, 1966).

Inasmuch as the first larval stage of *Palinurellus* is essentially a primitive palinurid phyllosoma, larval characters provide no support for the removal of *Palinurellus* from the Palinuridae, although such a removal might still be justifiable on the basis of adult structure. Despite the peculiarities of the adult, *Palinurellus* apparently is derived from an ancestor which had already acquired the characteristic larval form of the Scyllaridea.

As Gurney (1936) observed, the phyllosomas of some Scyllaridae bear a close resemblance to those of certain Palinuridae, while others are quite different. In all phyllosomas known or believed to belong to the Palinuridae, with the exception of *Jasus*, maxilliped 3 from the earliest stages possesses a setose exopod, although Crawford and de Smidt (1923) and Kinoshita (1934) did not report an exopod in stage I of *Panulirus argus* and *P. japonicus* respectively. Johnson (1956) called attention to the latter discrepancies arising "either from a considerable variability in the larval structures of some species or from erroneous descriptions." All available evidence indicates that Baisre (1966)

was correct in stating, "En la actualidad, no cabe duda acerca de la presencia de este exopodio, tanto en *P. argus* como en *P. japonicus*." The absence of the exopod in larvae of *Jasus* is well documented, however, and it is absent, or present only as a small rudiment in late stages, in all known phyllosomas of the Scyllaridae.

Lebour (1950) stated that the absence of the exopod on maxilliped 3 and the form of maxilla 2 "seem to be characters of undoubted value in the Scyllaridae." Baisre (1966) provisionally accepted these as "caracteres válidos en la separación de las larvas de ambas familias." In later stages of all known palinurid phyllosomas, including *Jasus*, the exopod of maxilla 2 is fringed with setae; in larvae of the Scyllaridae the exopod after the early stages is without setae. The only other character which holds good for the separation of the families, as Gurney (1936: 435) noted, "is the form of the antenna in the last stages." In his key to the phyllosomas of the DISCOVERY collection, he gave for the diagnosis of *Jasus*: "Antenna slender, with long flagellum;" and for the Scyllaridae: "Antenna enlarged at base, flagellum short and broad." This has proved to be somewhat misleading in that the characters refer to the later stages and are not applicable to the earliest stages.

In a recent paper dealing with larvae of *Jasus lalandii* from South Africa, Lazarus (1967) stated with reference to the Scyllaridae that "the larvae are distinguishable from those of the Family Palinuridae by the presence of a stout

second antenna, a foreshadowing of the broad, plate-like second antenna of the adult 'Shovel nose lobster'." He further stated (p. 13) that the Family Scyllaridae "is characterized by the flat antennae of the adults, a character visible even in the early phyllosoma stages (Fig. 9)." Lazarus evidently was not very familiar with larvae of the Scyllaridae, for the specimen illustrated in his fig. 9 (p. 11) is by no means an early phyllosoma; it appears in fact to be the final phyllosoma stage of a species of Scyllarus.

The first phyllosoma of Jasus as described by Archey (1916), Gilchrist (1916) and C. von Bonde (1936) from specimens hatched from the egg is remarkably similar to the corresponding stage of the scyllarid lobsters Parribacus antarcticus and Scyllarides aequinoctialis. I have not seen stage I of Jasus, but judged from the descriptions and illustrations given in the above works, each of which is more or less consistent with the others, the most salient diagnostic features of the first phyllosoma of Jasus are: (1) biramous antenna slightly longer than antennule; (2) endopod of antenna slightly longer than exopod, terminating in a tapering process regarded by Gilchrist as "the rudiments of the flagellum;" (3) antennule with a fairly prominent spine on the lateral margin in addition to a medial spine; (4) maxilliped 3 according to Gilchrist "consists of six distinct segments," although Archey's figure (p. 403, fig. 3) shows only five. The figure given by von Bonde (pl. 11, fig. 1), although not

acknowledged, appears to be a reproduction of Gilchrist's pl. 14. The corresponding characters of *Parribacus antarcticus* and *Scyllarides aequinoctialis* are: (1) biramous antenna somewhat shorter than antennule; (2) exopod of antenna slightly longer than endopod; (3) antennule with only a small medial seta; and (4) maxilliped 3 with five segments.

The planktonic phyllosoma 1.5 mm in length described by Lazarus (1967: fig. 1a) as stage I of *Jasus lalandii* agrees in each of the above points with *Parribacus* and *Scyllarides*, and differs from previous accounts of *Jasus* obtained from the egg. The same is true of two stage I phyllosomas 1.5 mm in length reported as *Jasus* by Prasad and Tampi (1959: 163, fig. 18). The latter were collected in the Indian Ocean at a latitude of 10°46'N. Prasad and Tampi called attention to the similarity of these specimens to one of the stage I phyllosomas from plankton described as *Scyllarides* by Lebour (1950), but considered them to be larvae of *Jasus lalandii*. It is clear that either the morphology of the first phyllosoma of *Jasus* must be quite variable, or that the planktonic specimens reported as stage I of *Jasus* by Lazarus and Prasad and Tampi have been misidentified. In my opinion, it is probable that Prasad and Tampi's specimens belong to *Parribacus antarcticus*, a common scyllarid in the Indian Ocean. This identification eliminates the necessity of assuming the occurrence of adults of *Jasus* at a tropical latitude in the Northern Hemisphere. As Prasad and Tampi pointed out, the genus is apparently confined to the cooler waters

of the Southern Hemisphere (southern circumpolar distribution, George and Main, 1967). Lazarus' material was collected off the southwest coast of South Africa, where Parribacus is not known to occur. It seems a reasonable possibility that his stage I may belong to Scyllarides elisabethae, although the main distribution of this species as given by Barnard (1950) is somewhat east of the area in which Lazarus found stage I.

The phyllosoma described by Lazarus as stage II of Jasus (fig. 1b) appears to agree with earlier accounts of the first phyllosoma of the latter. In view of these apparent discrepancies a re-examination of early larvae of Jasus from laboratory hatched material is desirable.

After the first few stages, one can readily distinguish phyllosomas of Jasus from those of all known Scyllaridae by the length of the antenna. The antenna in scyllarid phyllosomas is usually shorter, and never much longer than, the antennule, although in certain genera it remains slender until a considerable total length is attained.

The second articulation apparently present in maxilliped 3 in stage I of Jasus becomes obscure in later stages, and the appendage, as in phyllosomas of most if not all Scyllaridae, consists of only five distinct segments. The endopod of pereiopod 5 in Jasus becomes well developed, as in phyllosomas of Scyllarides aequinoctialis, Parribacus, ?Arctides and Ibacus, but the exopod appears only in the final stage as a minute bud. Gurney (1936) remarked that

the presence of an exopod on leg 5 is "perhaps primitive," and later (1942) stated that it "is a primitive feature retained also in the Nephropsidea."

George and Main (1967) regarded the presence or absence of a stridulating apparatus among the Palinuridae as indicating a major divergence within the family at an early stage of palinurid history. The nonstridulating line (Silentes) includes *Jasus* and the recently erected genus *Projasus* George and Grindley, 1964, established for *P. parkeri* (Stebbing) from the southeast coast of South Africa. All other palinurids (excluding *Palinurellus*) belong to the stridulating line (Stridentes).

I regard the absence of the exopod from maxilliped 3 in larvae of *Jasus* and its presence in all known larvae of other Palinuridae as evidence supporting the view of George and Main that the Palinuridae was divided into two divergent lines probably before the middle of the Mesozoic. In view of the similarity in other features between the first phyllosomas of *Jasus*, *Scyllarides* and *Parribacus*, I regard the absence of this exopod in larvae of all Scyllaridae as evidence of phylogenetic affinity between the latter and the Silentes group of Palinuridae, supporting the view of Boas, based on adult homologies, that the scyllarids are derived from a form related to *Jasus*. George and Grindley (1964) regarded *Projasus* as a genus "intermediate between *Palinurellus* and *Jasus*;" the latter was regarded by George and Main (1967) "as a derivative of *Projasus* emerging at or

before the Miocene . . . ." Since the Scyllaridae was established before the end of the Cretaceous, they may have been derived from palinurid stock near Projasus or between Palinurellus and the latter, before the appearance of Jasus. Needless to say the larval characters of Projasus would be of considerable interest.

Larvae of Jasus differ also from those of the Stridentes line of Palinuridae and resemble those of the Scyllaridae in the suppressed development of the exopod of maxilliped 2. This may be another feature indicating phylogenetic affinity, although as Gurney (1936: 420) noted, "The exopod of maxilliped 2 always develops late and its loss, even in a Palinurid, would not be surprising." The exopod nevertheless becomes relatively well developed and acquires setae sooner or later in the development of all larvae known to belong to the Stridentes, although in some species of Panulirus it does not become setose until the final phyllosoma stage. In larvae of Jasus and all Scyllaridae known, the exopod of maxilliped 2 in the final stage is only a small rudimentary bud.

The occurrence of a free-swimming prephyllosoma stage in Jasus, Ibacus and Scyllarides may not be without phylogenetic significance. None has been reported for any of the Stridentes, although the larvae of several genera are still unknown. It would be interesting to know if one occurs in Projasus and Palinurellus.

Adult scyllarid lobsters, with the exception in certain

respects of *Thenus*, by their general form appear to fall into one of two groups: (1) those with a carapace strongly depressed, broad, and with the lateral border deeply incised at the level of the cervical groove, including *Ibacus*, *Parribacus* and *Evibacus*; and (2) those with a carapace less depressed, narrower, and shallowly notched, including *Scyllarides*, *Arctides* and *Scyllarus*. In Bouvier's (1940: 87) opinion representatives of the first group:

> . . . sont primitifs et se rapprochent des Palinuridés brévicornes, surtout de *Jasus*; les *Scyllarides* ne le sont guère moins et au stade natant de *pseudibacus* ressemblent tout à fait aux précédents; les *Scyllarus* marquent le terme de l'évolution dans la famille mais, au stade natant de *nisto*, établissent par leur forme un passage entre les *Scyllarides* et l'adulte.

Saisho (1962b) has suggested that there are two types of first stage phyllosoma among the Scyllaridae: (1) the *Ibacus*-type, including *Ibacus* and *Thenus*; and (2) the *Parribacus*-type, including *Parribacus* and *Scyllarus*. *Scyllarides* and presumably *Arctides* would belong to the latter type. This grouping is based primarily on size and degree of development at hatching, and calls attention to the fact that *Ibacus* and *Thenus* hatch at a larger and more advanced stage. It apparently was not established necessarily to reflect phylogenetic affinities.

Comparison of early larvae of *Ibacus* with other genera is obscured because the early stages have been incorporated into the embryonic development, and the phyllosoma at

hatching is relatively advanced. Pereiopod 4 in stage I of *Ibacus* is fairly well developed, with a rudimentary exopod, and pereiopod 5 is already a rudiment longer than the abdomen, with a small exopod bud. The antenna is biramous and considerably shorter than the antennule; the endopod, in contrast to *Palinurellus*, *Jasus*, *Scyllarides*, *Parribacus* and ?*Arctides*, apparently lacks an articulation (Harada, 1958; Saisho and Nakahara, 1960; Dotsu, Seno and Inoue, 1966).

Dakin and Colefax (1940) gave an erroneous account of larvae of *Ibacus*. They identified "with at least *generic* certainty" planktonic phyllosomas 1.1 and 1.8 mm in length. Their identification was made by comparison of these specimens with the first phyllosoma, approximately 3 mm in length, of *Ibacus peronii* Leach hatched from the egg. As seen from their description and fig. 262, the phyllosomas of 1.1 and 1.8 mm undoubtedly belong to a species of *Scyllarus*.

The scyllarid phyllosomas possessing in later stages the greatest number of features in common with *Palinurellus* are those of *Ibacus*. Later larvae of *Ibacus* are the only scyllarid phyllosomas resembling *Palinurellus* in the possession of a cephalic shield which covers the entire thorax to the base of the abdomen. A unique feature of *Ibacus* is the presence of a longitudinal carina dorsally on each side of the cephalic shield. Pereiopod 5 in *Ibacus*, as in certain other scyllarid phyllosomas, becomes well developed and acquires a setose exopod at an early stage. A similarity

to *Palinurellus* is the appearance of gill buds of the podobranchia at least one and possibly two stages before the final phyllosoma (see Tokioka and Harada, 1963).

It appears therefore that phyllosomas of *Ibacus*, although specialized in certain respects, retain more of the primitive features characteristic of *Palinurellus* than any other scyllarid larva. This suggests that *Ibacus* may represent an early offshoot of the scyllarid stock, supporting Bouvier's view of the primitiveness of the genus. George and Main (1967) have noted a southern circumpolar distribution pattern of closely related species in *Ibacus* similar to that found in *Jasus*, although *Ibacus* occurs also in subtropical waters.

Larvae of *Thenus* as described by Prasad and Tampi (1957) hatch at a length just under 3 mm, with the endopod of pereiopod 4 well developed, but without an exopod, and pereiopod 5 a rudiment somewhat shorter than in *Ibacus*. The antenna is uniramous as in stage I of *Scyllarus*, and slightly longer than in the latter. In later stages pereiopod 5 becomes a rudiment somewhat longer than in phyllosomas of *Scyllarus*, but lacks an exopod. The latest stage reported by Prasad and Tampi (fig. 5) is 17.8 mm in length. It is curious in that all the gill buds are well developed and the antennae, mouthparts and other structures are characteristic of a final phyllosoma, but the pleopods are present only as small uniramous protuberances. Santucci's (1927: 192, pl. 3, figs. 2-4) specimen of 15 or 18 mm from

the northern end of the Red Sea, which I believe was correctly assigned to Thenus, has small but bilobed pleopods. Prasad and Tampi felt that their specimen "may represent a fairly advanced stage" and that there are two or three more stages. There is at least a possibility that the larva represents the final stage, but if Prasad and Tampi are correct, the presence of gill buds would be a resemblance to Palinurellus and Ibacus. The medial margin of the terminal article of the antenna and the lateral border of the outer process are distinctly serrated as in Ibacus. The fore-body is broadly subquadrate in outline but covers the thorax only to the level of the base of pereiopod 2. Prasad and Tampi's illustrations of all but the latest stage show maxilliped 3 with six segments, whereas in other Scyllaridae there are only five. The abdomen is not markedly broadened at the base and does not form a direct continuation of the hind-body as in Scyllarus.

The phyllosoma of Thenus, in possessing a uniramous antenna in early stages and in the reduction of the endopod and loss of the exopod of pereiopod 5, must be regarded as farther removed from the ancestral form than Ibacus. The definitive antenna is formed by differentiation of the endopod, and in most phyllosomas which possess a biramous antenna at hatching, the exopod in subsequent stages becomes progressively smaller and eventually disappears entirely. It may persist as a small process at the end of the basal antennal article in the final stage of some palinurid

phyllosomas. A biramous antenna appears to occur in phyllosomas of the more primitive representatives of both families. There seems to be a parallel evolutionary trend toward early loss of the exopod, since the antenna at hatching is uniramous in *Scyllarus* and *Panulirus*, the genera usually acknowledged on adult structure to be the most highly evolved in their respective families.

The adult of *Thenus* possesses a full gill complement of 21 pairs, and is unique among Scyllaridae in having the eye situated at the extreme outer angle of the carapace; in *Ibacus* the eyes are situated nearer to the midline of the carapace than to the outer angles. The carapace of *Thenus* is relatively broad and depressed, but the lateral border is not deeply incised as in *Ibacus*. By both adult and larval characters, *Thenus* may perhaps be regarded as a later and somewhat specialized derivative of the scyllarid line.

As shown earlier, larval characters place both *Parribacus* and *Scyllarides aequinoctialis* near the primitive scyllarid stem. The close similarity between their first phyllosomas indicates that *Parribacus* is more closely related to the latter than to *Ibacus*, despite the greater superficial resemblance between adults of *Parribacus* and *Ibacus*. Bouvier (1917) pointed out that a greater similarity exists between the first postlarval stage of *Parribacus* and *Scyllarides* than between the adults. Apparently *Parribacus*, along with *Ibacus* and *Evibacus*, has retained the original depressed form of the postlarva, whereas *Scyllarides* in

later stages diverges from the primitive form, the carapace assuming a more convex facies. The eyes in adults of both *Parribacus* and *Scyllarides* are situated nearer the outer angles of the carapace than to the midline.

A point of interest arising from the present study, if my identifications of planktonic phyllosomas are correct, is the existence of two species groups within the genus *Scyllarides*. In one, represented so far only by *S. aequinoctialis*, pereiopod 5 becomes well developed and acquires a setose exopod at an early stage. *Scyllarides astori* Holthuis, 1960, from the Galapagos Islands is similar to *S. aequinoctialis* and may belong to this group (see Holthuis and Loesch, 1967). The other group, in which pereiopod 5 in the larva remains a short rudiment, is apparently at a more advanced level of evolution, if the presence of a well developed pereiopod 5 with setose exopod can properly be regarded as a primitive feature. The latter group would include *S. nodifer*, *latus*, probably *herklotsii*, *delfosi* and some others. The fossil genus *Scyllarella* Rathbun, 1935, from the lower Eocene of the Alabama coastal plain resembles in certain features juvenile *Scyllarides nodifer*.

The phyllosomas tentatively identified in this study as *Arctides guineensis* resemble the phyllosomas of *Scyllarides*, especially in the earlier stages. According to Holthuis (1960), *Arctides* and *Scyllarides* are closely related; the mouthparts and branchial formula of the adult *Arctides* "are identical with those of *Scyllarides*." *Arctides* resembles

Scyllarus in having the distal antennal article cut into distinct teeth and in possessing sculpture on the abdominal somites. George and Main (1967) considered abdominal sculpture in the Palinuridae as well as in other groups "to be a random development rather than a phylogenetic indicator." The present example bears this out. Larval characters support the close relation of *Scyllarides* and *Arctides*; the possession of a well developed pereiopod 5 with setose exopod suggests that *Arctides* may be a derivative near the level of the *Scyllarides aequinoctialis* group.

Gurney (1936: 400) called attention to the marked differences between phyllosomas of *Scyllarus* (and erroneously *Scyllarides*) and those which he tentatively identified as "*Thenus*?" (probably *Scyllarides*) and "*Parribacus*?" He was disturbed by the resemblance between the last group and phyllosomas of certain Palinuridae, observing that if they were really Scyllaridae "there are two quite distinct types of scyllarid Phyllosoma. This would imply a separation of the Scyllaridae into two groups, a separation which cannot, so far as I know, be justified on adult structure." The similarity to the Palinuridae, especially to *Panulirus*, is primarily in the pear-shape and proportions of the fore-body, which in my opinion is a convergent feature without phylogenetic significance. There does appear to be some evidence for an evolutionary trend within the Palinuridae toward a pear-shaped fore-body. In the Scyllaridae the shape of the fore-body is known to very considerably among phyllosomas

of different species of Scyllarus.

Adult and larval structure indicate that Scyllarus in an evolutionary sense stands rather well apart from other Scyllaridae. The carapace is relatively convex and the location of the orbits is similar to Scyllarides, but in addition to their generally smaller size, species of Scyllarus have undergone a branchial reduction (from 21 to 19 pairs) along with a modification of the posterior two pairs of maxillipeds. Maxilliped 2 is without gills and its exopod is transformed into a lamellate process, while the exopod of maxilliped 3 has lost its flagellum. An analagous situation regarding the exopod exists in Panulirus, considered by George and Main (1967) to be the most recently evolved palinurid genus. Since all other palinurid genera have fully formed exopods of the second and third maxillipeds, those species of Panulirus with the most reduced exopods are regarded as the most advanced. Scyllarus may similarly be regarded as the most highly evolved genus of the Scyllaridae, as recognized by Bouvier (1917, 1940) and others.

The first phyllosoma of Scyllarus resembles Thenus in possessing a uniramous antenna. Later stages of the two genera are similar in that pereiopod 5 remains rudimentary, without an exopod. I interpret these features as indicative of a higher evolutionary level, but ones which may be acquired independently. Later stages known to be Scyllarus differ from all other phyllosomas in having an abdomen markedly broadened at the base, forming a direct, tapering

continuation of the hind-body (the "Phyllosomes laticaudes" of Milne-Edwards). The coxal segment of maxilliped 2 in the final phyllosoma of *Scyllarus* has no trace of an epipodite.

It might be justifiable from larval characters to suggest a close relationship of *Scyllarus* with *Thenus* were it not for the unique specimen described as "Phyllosoma Q" in the present study. This larva is of great interest from a phylogenetic point of view because the form of the abdomen is typical of all known phyllosomas of *Scyllarus* at a similar stage, but pereiopod 5 is well developed and possesses a setose exopod. The latter character is found in larvae of the more primitive scyllarids and in the most primitive palinurids, but is unknown in any phyllosoma of *Scyllarus*. The specimen also possesses a remarkable combination of other characters. The form of the antenna and of maxilla 2 are typical of *Scyllarus*, while the shape and proportions of the fore-body and the length of the eyestalk are characteristic of *Parribacus* and *Scyllarides*. I suggest therefore that this phyllosoma, whatever its identity may prove to be, provides evidence for the derivation of *Scyllarus* from a relatively primitive scyllarid ancestor related to *Parribacus* and *Scyllarides aequinoctialis*. Although pereiopod 5 is reduced to a rudiment in larvae of the presumably more advanced species of *Scyllarides* as well as in *Scyllarus*, the presence in this specimen of a well developed pereiopod 5 with setose exopod may exclude the former from the direct ancestry of *Scyllarus*.

I have been unable to account for the larvae of Scyllarus faxoni in the present investigation. There is a possibility that the unique phyllosoma might belong to this species. Bouvier (1940) noted that the characters of Scyllarus at the postlarval stage are close to the adult, but the postlarva does not yet show the sculpture on the abdominal segments present in the adult of most species. He regarded as the most primitive species those conserving in the adult the lack of arborescent sculpture, including S. faxoni. The latter apparently differs also from most other species of the genus in that the third maxillipeds are inserted nearly at the same level as the anterior border of the thoracic sternum. There are additional differences in the legs. Since "Phyllosoma Q" appears to be a link between the Scyllarides-Parribacus type of phyllosoma and Scyllarus, it reasonably might belong to the most primitive western Atlantic species of the latter.

S. faxoni is a relatively deep water species, which may attain a depth of 200 fathoms. According to Bouvier (1925) it is closely related to the Indopacific S. rubens Alcock and Anderson, which occurs between 142 and 400 fathoms. Scyllarus is presently represented by well over 30 species (see Harada, 1962; Holthuis, 1963), most occurring at lesser depths. These data may reflect a pattern of evolution from deeper to shallower water within the genus Scyllarus similar to that found within the family Palinuridae by George and Main (1967), and a radiation

paralleling that of *Panulirus*. I am aware, however, of no geological evidence for equatorial connections between the Atlantic and Pacific Oceans during the Pleistocene, which George and Main have postulated to account for speciation in *Panulirus*.

Length of larval life and number of stages. Until now the length of larval life and the number of phyllosoma stages have not been known with certainty for any scyllaridean lobster. Saisho (1962b) stated that "in comparison with the palinulid [sic] the scyllarid phyllosoma shows a rapid development; the free-swimming life is somewhat shorter, and larval ecdyses are fewer in frequencies than the palinulid [sic] phyllosoma." This generalization is probably true of the genus *Scyllarus*, in which the progressive morphological development occurring at each ecdysis is greater and the intermolt period shorter than that of early stages of *Panulirus* cultured in the laboratory (see Saisho and Nakahara, 1960; Saisho, 1962a; Inoue and Nonaka, 1963; Johnson and Knight, 1966; Ong, 1967). The complete larval development of various species of *Panulirus* is generally thought to require at least six months. In the genus *Scyllarus* the total duration of larval life is now known to range from little over a month for *S. americanus* to probably three or four months for species such as *S. arctus*, *S. nearctus* and *S. bicuspidatus*. Larvae of the last species reared by Saisho (1966b) lived for a maximum of 78 days and reached a ninth stage (p. 199, fig. 5),

which was only 4.8 mm in length and still in an intermediate phase of development.

Those species of *Scyllarus* having the shortest larval histories would be among the 70 per cent of marine decapods estimated by Thorson (1961) to require "less than 5 weeks for their pelagic development." The relatively short larval life of *Scyllarus* may be in part a compensation in larval survival for the lower fecundity accompanying the small adult size. The number of eggs carried by *Panulirus*, as well as the species of large scyllarid lobsters, appears to be roughly 10 to 100 times that of *Scyllarus*.

In recent years it has become apparent that, because of the gradual morphological changes in the development of *Panulirus*, there is little correspondence between the number of ecdyses and the intermediate and later "stages" generally recognized in studies of planktonic material (Johnson and Knight, 1966; Saisho, 1966a). Johnson and Knight have suggested that *P. inflatus* (Bouvier) may undergo up to 25 or more ecdyses in attaining the final phyllosoma stage. Because of the more marked morphological advances at each ecdysis in the development of *Scyllarus*, as well as the smaller number of stages, one can, in at least some species, recognize stages from the plankton which do correspond more or less to those obtained in the laboratory.

The number of phyllosoma stages in the larval history apparently varies from about six to ten or more among different species of *Scyllarus*. Stephensen (1923) and Santucci

(1925) recognized nine stages from the plankton in the development of S. arctus. Prasad and Tampi (1957) suggested nine stages for the species which they designated "Scyllarus sp. B." In a later study of planktonic material from the Arabian Sea, Prasad and Tampi (1960a) believed there to be ten phyllosoma stages in the development of two other species of Scyllarus. It appears to me that Prasad and Tampi were inclined in certain instances to overestimate the number of stages. Judged from their figures and measurements, this may be the case in their "Scyllarus sp., I." The phyllosoma designated "Scyllarus sp., IV" appears to be a subfinal stage, with the rudiments of the gills indicated, and it is doubtful that "there might occur two more stages" before the postlarval stage. Al-Kholy (1960) stated that the life history of S. thioriouxi Bouvier consists of five larval stages, which were obtained from plankton to the Red Sea (no justification is given for the identification of the phyllosomas). Judged from the difference in length and morphological development between his stages III and IV, it seems likely that there is an additional stage. The present investigation indicates six or seven stages for S. americanus, six for S. chacei, probably seven for Scyllarus n. sp., and nine or ten for S. nearctus. The stage IX of S. bicuspidatus obtained in the laboratory by Saisho (1966b) was still in an intermediate stage of development, so unless growth was significantly retarded, there would be a total of more than ten stages.

Evidence indicates that many other scyllarid lobsters, including *Scyllarides*, *Parribacus*, ?*Arctides* and possibly *Ibacus* may have a larval life as long as, if not longer than, that of palinurid lobsters. Saisho and Nakahara (1960) obtained stage IV of *Ibacus ciliatus* after about one month of rearing at 23.5°-28.4°C on a diet of brine shrimp nauplii. Phyllosomas of this species and *I. novemdentatus* fed larval gobiid fishes were only in the third or fourth stage after nearly two months at 18°-22°C (Dotsu, Seno and Inoue, 1966). The first four stages of *Ibacus* are well defined morphologically; the intermediate stages have yet to be reported. Tokioka and Harada (1963: 262) mentioned evidence relating to the seasonal occurrence of the final stage which, although admittedly fragmentary, implies that the complete larval development of *Ibacus* may require one year or more.

In *Scyllarides*, *Parribacus* and ?*Arctides* there seem to be numerous ecdyses as in *Panulirus*, and specimens from the plankton after the early stages no longer fall into well defined stages of morphological development, with the exception of the final and perhaps the subfinal stage. In the absence of empirical data concerning the growth factor at various phases of the life history, predictions based on formulas such as that of Brooks are, as Sims (1965a) has pointed out, generally "inadequate to show the true number of stages."

In recent years it has become increasingly clear that the number of larval stages in the development of many

decapods may vary (Broad, 1957; Provenzano and Dobkin, 1962; Boyd and Johnson, 1963; Costlow, 1965; Ewald, 1965; Knowlton, 1965). Temperature and the amount of available food are known to be important factors affecting rate of larval development; other things being equal, a well-fed larva will be farther advanced in the next stage than a poorly fed one. This effect is often seen in comparison of reared phyllosomas with those from the plankton. Costlow (1963) found evidence that molting and growth of blue crab megalops were independent and controlled by separate endocrine systems, and later (Costlow, 1965) suggested that insufficient food, dietary deficiencies or the absence of certain trace elements in sea water could prevent or delay the normal function of the endocrine mechanisms which control development. He stated, "Externally these deficiencies, as well as the resulting malfunctioning of the endocrine system, would be manifest as variability in the number of larval stages or in minor differences in morphological characters of the larvae." One might expect such variation to be the rule rather than an exception among scyllaridean lobsters. Phyllosoma larvae in their relatively long pelagic life would be likely to encounter variations in environmental parameters as well as in the availability and perhaps the kind of food which could alter the number of stages in the course of development.

Johnson and Knight (1966) called attention to the problem in reporting a study of larvae arising from "a considerable

number of difficult-to-determine instars in the phyllosoma period contrasted with the arbitrary assignment of stages . . . . " They felt that for practical ecological studies it was best to retain the concept of stages which "may include a range of characteristics implying one or more instars but that still depict comparable steps in the life history of the larvae in nature." This is especially true for the more intensively studied genera such as Panulirus and Jasus. Since size is equally convenient and also of diagnostic value in many instances, I prefer for descriptive purposes in reporting previously little known forms to designate the phyllosoma, as Saisho (1966b) has done, by its total length. A key to the recognition of arbitrarily assigned stages may be provided for those species which are represented by a fairly complete developmental sequence.

Survival of phyllosomas at low temperature. Sims (1968) has recently considered the possibility of phyllosomas surviving at the lower temperatures of relatively high latitudes in the North Atlantic, "where larval development is probably slowed as the water cools and great mortality must occur." He reported specimens collected as far north as latitude 41°33', at a temperature of 18.6°C. Results of the present investigation indicate that larval development of the species reared can proceed, with a longer duration, at 20°C. Early phyllosomas can live for weeks at 15°C, although molting is severely inhibited or prevented entirely. A temperature of 10°C was usually lethal within one or two

weeks; larvae surviving longer than one week were in extremely poor condition and could not be expected to live in nature.

Rearing of phyllosoma larvae in the laboratory. Gurney (1942) pointed out that "A certain amount of caution is necessary in accepting a series of stages as determined under artificial conditions as normal." Results of the present investigation indicate that reared phyllosomas tend to be somewhat smaller and less develop morphologically at a given stage than specimens from the plankton. There is the possibility, therefore, that reared individuals may require more molts than larvae in nature to reach the same stage of morphological development. The results of rearing two different broods of Scyllarides aequinoctialis suggest that only a certain degree of morphological development was possible under the experimental conditions. The most morphologically advanced stage obtained on both occasions was essentially the same, even though survival in the second experiment was much better because of improved controls. Toward the end of each experiment I observed instances of molting without much advance in morphology, together with a small growth factor.

Attempts to culture phyllosoma larvae of the Japanese spiny lobster Panulirus japonicus, as well as my work with P. argus and P. guttatus, indicate that brine shrimp nauplii are a satisfactory food for the early stages, but that little further progress can be expected in rearing larvae of Panulirus until it becomes possible to provide a more suitable diet for the later stages (see Inoue and Nonaka, 1963; Inoue,

1965; Saisho, 1966a). The same is no doubt true of Scyllarides, Parribacus and most other genera. Saisho (1966a) reported larvae of Panulirus japonicus reared to a maximum length of only 8 mm after 178 days and 16 molts. Development in this instance must have been arrested.

Ong (1967) called attention to the possibility that phyllosomas may have a shorter intermolt period in nature than in the laboratory. Most rearing experiments, including those of the present study, have shown a longer intermolt period in later stages. Starvation usually inhibits molting among crustaceans in general (Passano, 1960). The extent of possible abnormality in the duration of larval life observed in the laboratory, resulting from inadequate diet or other less than optimum conditions, is difficult to assess. Inoue (1965) found that at water temperature between 22° and 28°C the quantity of food taken by early phyllosomas (up to stage IV) of Panulirus japonicus was one Artemia nauplius per hour. He suggested that it is possible to culture phyllosomas in a "state of repletion" by maintaining a density of four brine shrimp nauplii per ml of water, but pointed out that the size of the food should be altered with the stage of the phyllosoma. Saisho (1966a) found that the interval between molts of phyllosomas of P. japonicus usually "becomes shorter when more or better food is provided. . . . " He showed (Saisho, 1966b: 191, Table 6) that the intermolt period of the first three stages of this species was considerably shortened when the density of brine shrimp nauplii was

increased from 3-5 to 30-40 per cc.

Early phyllosomas appear to feed on *Artemia* nauplii by catching them on the spines near the ends of the pereiopods and transferring them to the mouth region. Later phyllosomas seem to have difficulty catching brine shrimp nauplii. In view of the changes in size and morphology of phyllosomas during their development, it seems likely that their food and feeding habits may vary at different phases of the larval history. The mouthparts of larger phyllosomas are relatively small in relation to the overall size of the animal, but they do not appear adapted for capturing small planktonic organisms.

The observed reduction in growth and high mortality in later stages of reared larvae in general, as well as my failure to obtain postlarvae of any species other than *S. americanus*, can probably be attributed at least in part to either a qualitative deficiency in the diet of *Artemia* nauplii or the inability of the phyllosomas to capture sufficient quantities, or both. The successful rearing of *S. americanus* to the postlarva is probably related to the fact that larval development of this species in nature takes place in coastal waters, as well as to a combination of other factors, including the relatively short larval life, small number of stages, small size of the final phyllosoma and hardiness of the larvae.

Natural food of phyllosoma larvae. One of the major deficiencies in our knowledge of the larval development of

scyllaridean lobsters is the virtually complete lack of information concerning the natural food of phyllosomas. The latter are known to be carnivorous, but their feeding habits in nature remain obscure. A phyllosoma of Palinurus in a plunger jar was seen by Lebour (1925) to catch and eat larval anglerfish. She mentioned that it ate copepods, although it was never actually seen to catch them. Phyllosomas of Ibacus fed living larvae of gobiid fishes reached the third or fourth stage, but the number surviving was low (Dotsu, Seno and Inoue, 1966). Saisho (1966b) experimented with a variety of potential foods, both natural and artificial, but apparently found none more satisfactory than brine shrimp nauplii. I obtained negative results in attempts to feed stage I phyllosomas of Scyllarides aequinoctialis with fertilized embryos of the urchin Lytechinus variegatus.

Thomas (1963) and Shojima (1963) reported phyllosomas of Ibacus attached to scyphozoan medusae, but the significance of this association is not clear. Thomas stated that "it was not clearly demonstrated that they were actually feeding on the medusae," but "the fact that the general body structure of the late stage larvae was coloured with the same purple pigment as that in the medusa suggests that they were." Dr. D. I. Williamson (reported by Thomas, 1963) was able to feed phyllosomas of Jasus on hycromedusae. Williamson was convinced that the latter are a natural food of early palinurid phyllosomas and possibly of later stages (Williamson, personal communication, 1964). He observed

larvae swimming with the medusae held by and trailing from the third pereiopods. Shojima (1963) collected phyllosomas of Scyllarus carrying hydromedusae in a similar manner.

In the present study phyllosomas of Scyllarides aequinoctialis, offered planktonic heteropods and immobilized chaetognaths, would often seize them by the ends of the pereiopods and then swim about, from time to time holding the organisms against the mouth region; it appeared, however, that little or nothing was ingested. One suspects that the elongated, blade-like dactyl of pereiopod 3 in later phyllosomas of Scyllarides, Parribacus and ?Arctides may in some way be associated with their feeding habits; perhaps it is used to impale or cling to relatively large and slow-moving organisms such as medusae.

The prospects at this time for rearing most scyllaridean lobsters through their complete larval development in the laboratory are not encouraging. Further studies on the feeding of phyllosoma larvae are needed. In the meantime the technique used in the present investigation provides a reliable method for rearing phyllosomas through at least several early stages of development, making possible systematic and ecological studies.

Systematic problems remaining. The most outstanding systematic problems remaining in our knowledge of the larvae of western Atlantic Scyllaridae are briefly: (1) confirmation of my identifications of Scyllarides nodifer, Parribacus antarcticus and Arctides guineensis by rearing larvae

from the egg, and recognition of diagnostic features of the early stages; (2) establishing the larval characters of the South American species of *Scyllarides*; (3) identification of the phyllosomas of *Scyllarus faxoni*; and (4) discovery of a sequence of stages in the development of "Phyllosoma Q" and identification with the parent species.

PART VI

KEYS

Provisional Key for the Generic Determination of Phyllosoma Larvae (World-Wide)

The most comprehensive key in existence to the various forms of phyllosoma larvae is by Gurney (1936: 439), based only on the DISCOVERY material. In the following key I have attempted to bring together the most recent information available, including results of the present investigation. In using this key one must bear in mind its incompleteness and other limitations. No information is available for Evibacus among the Scyllaridae nor for Projasus, Linuparus or Palinustus among the Palinuridae. Some identifications are at best tentative. In few instances are the generic characters based on all species of a genus. It is difficult to give characters which pertain to all stages of forms for which only a few stages have been described. I have not included the form from the western Indian Ocean attributed by Gurney (p. 403, fig. 15) to Palinurus sp. A smaller specimen also from that region, belonging probably to the same species, has been designated "Panulirus sp. V" by Prasad and Tampi (1959: 159, fig. 16). In my opinion both of these

identifications are dubious; the likelihood that this form may belong to *Linuparus* or *Palinustus* seems greater. The form described in the present study as "Phyllosoma Q" is not included in the key because the characters of the other stages are unknown. The diagnosis of ?*Justitia* is from my unpublished data on planktonic material collected in the western Atlantic. The character given for *Panulirus* in Gurney's key, *viz*. hind-body wider than fore-body, is not valid for all species (e.g. *Panulirus penicillatus* Olivier, Prasad and Tampi, 1959; *Panulirus inflatus* (Bouvier), Johnson and Knight, 1966).

1. Maxilliped 3 with setose exopod 2
Palinuridae (Stridentes); *Palinurellus*

Maxilliped 3 without exopod, or with small rudiment only 6

2. Antenna in early stages biramous; fore-body in subsequent stages covering all of thorax 3

Antenna in early stages uniramous, or only with small process laterally near base; fore-body in subsequent stages not covering much more than base of pereiopod 1 4

3. A small rostrum present; fore-body more or less quadrate in outline . . . . *Palinurellus*

Rostrum absent (?); fore-body broadly oval or subcircular . . . . ?*Puerulus*

4. Antenna with small process laterally near base; fore-body about 1.5 times wider than hind-body; maxilla 2 with small palp; endopod of pereiopod 4 more or less rudimentary . . . . *Palinurus*

Antenna without lateral process; fore-body often narrower, never much more than 1.2 times wider, than hind-body; maxilla 2 usually without palp; endopod of pereiopod 4 becoming well developed or remaining rudimentary 5

5. Pereiopod 4 after early stages with setose exopod, but endopod remaining a short rudiment; hind-body after early stages about twice as broad as long; fore-body in early and intermediate stages crossing hind-body about midway between base of maxilliped 2 and maxilliped 3, in last stages still well anterior to base of maxilliped 3 . . . . ?*Justitia*

Endopod of pereiopod 4 becoming relatively well developed; hind-body less than twice as broad as long; fore-body usually crossing hind-body near or beyond base of maxilliped 3 . . . . *Panulirus*

6. Antenna in earliest stages biramous, longer than antennule; antennule with a spine laterally; antenna in subsequent stages slender, with long flagellum . . . . *Jasus* (Palinuridae, Silentes)

Antenna in earliest stages, if biramous, not longer than antennule; antennule without lateral spine; antenna in subsequent stages short, in late stages broad . . 7 (Scyllaridae)

7. Antenna in early stages uniramous; fore-body becoming subcircular or subquadrate in outline, much broader than hind-body; pereiopod 5 never with setose exopod 8

Antenna in early stages biramous; fore-body pear-shaped or semielliptical in outline, or, if broadly subquadrate, pereiopod 5 with setose exopod at early stage 9

8. Pereiopod 4 well developed in earliest stages; rudiment of pereiopod 5 becoming somewhat longer than abdomen at early stage; abdomen in later stages not much broadened at base; medial margin of antennal flagellum serrated . . . . *Thenus*

Pereiopod 4 rudimentary in earliest stages; rudiment of pereiopod 5 never much longer than abdomen; latter in later stages broad at base, forming tapering continuation of hind-body; antennal flagellum not distinctly serrated . . . . *Scyllarus*

9. Fore-body broadly subquadrate in outline; in later stages covering entire thorax, with two serrated longitudinal ridges dorsally; length up to 46 mm . . . . *Ibacus*

Fore-body usually pear-shaped or semielliptical in outline, never with dorsal ridges; length of final stage from 36 to 80 mm 10

10. Pereiopod 5 a small bud or short rudiment, never with setose exopod . . . . *Scyllarides*
(*latus*, *nodifer*, ?*herklotsii*, ?*delfosi*, ?spp.)

Pereiopod 5 becoming well developed at early stage, with setose exopod by TL 9-10 mm 11

11. Fore-body by TL 7-8 mm slightly narrower than hind-body, eyestalk 1.7-2.0 times length of antennule; fore-body in subsequent stages becoming much narrower than hind-body . . . . ?*Arctides*

Fore-body by TL 7-8 mm slightly broader than hind-body, eyestalk not more than 1.5 times length of antennule; fore-body in subsequent stages somewhat broader than hind-body 12

12. Antenna from TL about 9 through 35 mm uniramous, without exopod or lateral process; antenna and abdomen little developed before TL 40 mm; length of final stage 75-80 mm . . . . *Parribacus*

Antenna in intermediate stages with reduced exopod, later with lateral process; length of final stage not much over 40 mm . . . . *Scyllarides*
(*aequinoctialis*, ?spp.)

Provisional Key for the Generic Determination of Stage I Phyllosomas (World-Wide)

A separate key to stage I phyllosomas may prove useful. In all known stage I phyllosomas, there is no division or articulation between the cylindrical peduncle (stalk) on which the eye is borne and the eye itself. In all subsequent stages, with the possible exception of *Thenus orientalis* (see Prasad and Tampi, 1957), such a division is present.

This key is subject to the same limitations as the preceding key. Baisre (1966: 25) gave a key for the stage I phyllosomas of the Scyllaridae. He used for the diagnosis of *Ibacus*: "Antenas y anténulas, ambas birramosas." I have given instead characters of the pereiopods, since in the first phyllosoma of *I. ciliatus* (see Dotsu, Seno and Inoue, 1966) the antennule does not appear to be truly biramous, having a prominent medial spine. The length of the telson spines, used by Baisre for distinguishing *Scyllarides* from *Parribacus*, is not a valid character. The characters given herein are based on *S. aequinoctialis* and *P. antarcticus*, and may not hold good for other species. ?*Arctides* would probably key out to either *Scyllarides* or *Parribacus*.

1. Maxilliped 3 with setose exopod 2
Palinuridae (Stridentes); *Palinurellus*

Maxilliped 3 without exopod 6

2. Antenna biramous 3

Antenna uniramous 4

3. Small rostrum present . . . . *Palinurellus*

No rostrum (?) . . . . ?*Puerulus*

4. Exopod of pereiopods 1-2 with 5 pairs of natatory setae; exopod of pereiopod 3 a small bud 5

Exopod of pereiopods 1-2 with more than 5 pairs of setae; exopod of pereiopod 3 an elongated rudiment . . . . *Palinurus*

5. Antenna at least half length of antennule. . . *Panulirus*

Antenna less than half length of antennule . . ?*Justitia*

6. Antenna biramous 7

Antenna uniramous 10

7. Antenna slightly longer than antennule; antennule with a spine laterally . . . . *Jasus* (Palinuridae, Silentes)

Antenna somewhat shorter than antennule; antennule with no spine or seta laterally . . . . 8 (Scyllaridae)

8. Pereiopod 4 well developed; exopod of pereiopod 3 setose . . . . *Ibacus*

Pereiopod 4 only a minute bud at base of abdomen; exopod of pereiopod 3 without setae 9

9. Exopod of pereiopods 1-2 with 6 pairs of natatory setae; total length about 1.9 mm . *Scyllarides*

Exopod of pereiopods 1-2 with 5 pairs of natatory setae; total length 1.5-1.6 mm . . *Parribacus*

10. Pereiopod 4 well developed; exopod of pereiopod 3 setose . . . . *Thenus*

Pereiopod 4 only a minute bud at base of abdomen; exopod of pereiopod 3 without setae . . . . *Scyllarus*

Provisional Key to the Phyllosoma Larvae of Western Atlantic Scyllaridae

No information is available for larvae of *Scyllarides deceptor*, *Scyllarides delfosi*, *Scyllarides brasiliensis* or *Scyllarus faxoni*. Diagnostic features of early stages of *Scyllarides* spp., *Parribacus antarcticus* and ?*Arctides guineensis* are unknown. The form described in the present study as "Phyllosoma Q" is not included in the key.

1. Maxilliped 3 with setose exopod . . . . Palinuridae

   Maxilliped 3 without setose exopod 2

2. Antenna in early stages uniramous; fore-body becoming subcircular or subquadrate in outline, not much longer than wide; abdomen in later stages broad at base, forming tapering continuation of hind-body; length up to 27 mm 3

   Antenna in early stages biramous; fore-body usually pear-shaped or semielliptical in outline, considerably longer than wide; abdomen through TL 27 mm narrow, after early stages situated in posterior concavity of hind-body; length up to 80 mm 6

3. Exopod of pereiopod 2 in first two stages respectively with 8 and 9 pairs of natatory setae; apical article of maxilla 2 with three setae; fore-body in subsequent stages subcircular in outline . . . . . . *Scyllarus americanus*

   Exopod of pereiopod 2 in first two stages respectively with fewer than 8 and 9 pairs of natatory setae; apical article of maxilla 2 often with four setae; fore-body in subsequent stages more or less subquadrate or trapezoidal in outline 4

4. Exopod of pereiopod 2 in first two stages respectively with 5 and 6 pairs of natatory setae; medial spine of antennule long; telson spines in subsequent stages elongated; late stages with spine dorsally at edge of hind-body adjacent to insertion of pereiopods

1-4; length of last two stages greater than 14 mm . . . . *Scyllarus nearctus*

Exopod of pereiopod 2 in first two stages respectively with more than 5 and 6 pairs of natatory setae; medial seta of antennule short; telson spines in subsequent stages not elongated; no spines dorsally at edge of hind-body; length of final stage less than 14 mm 5

5. Exopod of pereiopod 2 in stage I usually with 6½-7 pairs of natatory setae; eye and stalk in later stages 1.1-1.4 times length of antennule; larvae distinguished with difficulty from *Scyllarus* n. sp. . . . *Scyllarus chacei*

Exopod of pereiopod 2 in stage I with 6 pairs of natatory setae; eye and stalk in later stages 1.4-1.6 times length of antennule; larvae distinguished with difficulty from *Scyllarus chacei* . . . . . *Scyllarus* n. sp.

6. Pereiopod 5 recognizable by TL 4-5 mm as low, undeveloped bud; in subsequent stages remaining rudimentary, never with setose exopod 7

Pereiopod 5 by TL 5-6 mm a somewhat elongated bud; in subsequent stages becoming well developed, with setose exopod by TL 9-10 mm 8

7. Fore-body in later stages more or less oval in outline, narrowing gradually toward anterior end; pereiopod 5 in final stage not longer than abdomen; length of final stage about 37 mm . . . . *Scyllarides nodifer*

Fore-body in later stages relatively broader anteriorly, narrowing more abruptly at anterior end; pereiopod 5 in final stage longer than abdomen; length of final stage 51 mm . . . . *Scyllarides* sp.

8. Fore-body by TL 6-7 mm slightly narrower than hind-body; eyestalk/antennule ratio at TL 6-7 mm 1.5-1.8; at TL 7-8 mm 1.7-2.0; fore-body in subsequent stages becoming much narrower than hind-body . . . . ?*Arctides guineensis*

Fore-body by TL 6-7 mm slightly wider than hind-body; eyestalk/antennule ratio at TL

6-7 mm 1.2-1.4; at TL 7-8 mm 1.4-1.5; fore-body in subsequent stages somewhat broader than hind-body 9

9. Antenna from TL about 9 to 35 mm uniramous, without indication of exopod or lateral process; antenna and abdomen little developed before TL 41 mm; length up to 80 mm . . . . Parribacus antarcticus

Antenna with remnant of exopod up to TL 21-22 mm, then with lateral process; length up to 41 mm . . . . . Scyllarides aequinoctialis

Keys to the Identification of Stages

The following keys may be used for the identification of stages in reporting larvae of *Scyllarides aequinoctialis* and *Scyllarides nodifer* from the plankton. The first four stages given below, the specific and even generic differences of which are unknown, correspond to the actual number of molts. Later stages are arbitrarily designated by conspicuous features to depict, as Johnson and Knight (1966) have suggested, "comparable steps in the life history of the larvae in nature."

Key to the Identification of Phyllosoma Stages I-IV of *Scyllarides* spp., *Parribacus antarcticus* and ?*Arctides guineensis*

1. Eyes unstalked . . . . Stage I

Eyes stalked 2

2. Exopod of pereiopod 3 not setose . . . . Stage II

Exopod of pereiopod 3 setose 3

3. Pereiopod 4 a short, unsegmented rudiment . . Stage III

Pereiopod 4 more or less distinctly segmented . . . 4

4. Exopod of pereiopod 4 not setose . . . . Stage IV

Exopod of pereiopod 4 setose 5
(see separate keys below)

Key to the Identification of Later Phyllosoma Stages of *Scyllarides aequinoctialis*

5. Pereiopod 5 not more than twice length of abdomen . . . . Stage V

Pereiopod 5 more than twice length of abdomen 6

6. Exopod of pereiopod 5 not setose . . . . Stage VI

Exopod of pereiopod 5 setose 7

7. Maxilliped 1 not distinct . . . . Stage VII

Maxilliped 1 a more or less distinct bud or larger 8

8. Uropods uniramous buds . . . . Stage VIII

Uropods bilobed 9

9. Pleopods uniramous buds . . . . Stage IX

10. Inner ramus of uropod not extending beyond end of telson . . . . Stage X

Inner ramus of uropod extending slightly beyond end of telson 11

11. No gill buds . . . . Stage XI

Gill buds present . . . . Stage XII

Key to the Identification of Later Phyllosoma Stages of *Scyllarides nodifer*

5. Exopod of pereiopod 4 with 6 or fewer pairs of natatory setae . . . . Stage V

Exopod of pereiopod 4 with more than 6 pairs of natatory setae 6

6. Maxilla 2 with apical setae . . . . Stage VI

Maxilla 2 without apical setae 7

7. Antennular peduncle with only two distinct segments . . . . Stage VII

Antennular peduncle with three more or less distinct segments 8

8. Uropods uniramous buds . . . . Stage VIII

Uropods bilobed 9

9. Pleopods uniramous buds . . . . Stage IX

Pleopods biramous 10

10. Endopod of pleopods externally without distinct appendix interna . . . . Stage X

Appendix interna a small but distinct external protuberance 11

11. No gill buds . . . . Stage XI

Gill buds present . . . . Stage XII

PART VII

SUMMARY AND CONCLUSIONS

The objectives of this investigation have been to recognize and define the generic and specific characters of the phyllosoma larvae of western Atlantic scyllarid lobsters, to identify these larvae with the parent species, and to obtain data concerning their life histories. A number of phyllosomas collected in plankton were examined. Larvae of four species of _Scyllarus_ and one species of _Scyllarides_ were hatched in the laboratory and reared on a diet of brine shrimp nauplii. Various stages of the different phyllosomas are described and illustrated. The postlarval stage of three species of _Scyllarus_ obtained through metamorphosis of final phyllosomas in the laboratory is described. A provisional diagnosis is given for the larvae of each species. Keys are provided for the generic determination of phyllosoma larvae on a world-wide basis and for the specific identification of larvae of western Atlantic Scyllaridae insofar as the present state of our knowledge allows. Results of rearing experiments concerning growth, number of larval stages and length of larval life are presented, including the first successful attempt to rear the larvae of any scyllaridean lobster from hatching to the postlarva. Phylogenetic

affinities within the Scyllaridea are discussed in relation to larval characters. The literature dealing with phyllosoma larvae is reviewed and integrated in the light of present findings. The results are summarized below.

1. *Scyllarus americanus*. Larvae were reared from hatching to the postlarva. The larval life consists of six or seven phyllosoma stages and is of relatively short duration. Postlarvae were obtained at three salinities at 25°C in a minimum of 32 and a maximum of 40 days after hatching. *S. americanus* was the most common phyllosoma in waters of the Tortugas Shelf. Distributional data indicate that the entire larval development takes place in coastal waters, and that some spawning may occur throughout the year, with a peak in the spring and summer. Phyllosomas in stage I are characterized by the relatively great total length (1.5-1.7 mm), the large number of pairs of natatory setae on the exopod of pereiopod 2 (8), and the presence of only three apical setae on maxilla 2. Later stages are distinguished by the subcircular outline of the fore-body. Neither *Scyllarus depressus* (Smith, 1881) nor the specimen described by Bouvier (1925) are postlarval stages of *S. americanus*.

2. *Scyllarus nearctus*. Larvae were hatched in the laboratory and reared through seven stages. Three rather well defined later stages, including the final phyllosoma, were taken in plankton. Stage I is characterized by the long medial spine of the antennule, the small number of pairs of natatory setae (5) on the exopod of pereiopod 2, and by a

prominent chromatophore on each side of the fore-body. Intermediate stages are characterized by the elongated telson spines and the length of the antenna. Late stages are distinguished by their large size (14 to 27 mm) and by the presence of a dorsal spine at the edge of the hind-body adjacent to the insertion of pereiopods 1-4. The duration of each of the first five stages at 25°C was about seven days; the total duration through stage VII was 54 days. Phyllosomas were collected in plankton from January through May; postlarvae were taken in late March, April and May. Complete larval development is estimated to require three to four months. Postlarvae were obtained through metamorphosis of final phyllosomas in the laboratory. *Arctus depressus* and the postlarva reported as *S. americanus* by Bouvier (1925) appear to be postlarvae of *S. nearctus*.

3. *Scyllarus chacei*. Larvae were hatched in the laboratory and reared to the final phyllosoma in stage VII. A final phyllosoma collected in plankton metamorphosed to the postlarva in the laboratory. Comparison of reared with planktonic larvae indicates that the larval history in nature consists in most instances of only six phyllosoma stages. Stage I is distinguished from *S. americanus* by the slightly smaller length and by the possession of 6-7 pairs of natatory setae on the exopod of pereiopod 2 and of usually four apical setae on maxilla 2. Stage I of *S. chacei* differs from *S. nearctus* by the slightly greater length, the small medial seta of the antennule, and the larger number of pairs

of natatory setae on the exopod of pereiopod 2. Subsequent stages of *S. chacei* are characterized by the subquadrate or trapezoidal outline of the fore-body together with the relatively short telson spines. Phyllosomas of *S. chacei* closely resemble those of *Scyllarus* n. sp. The postlarva closely resembles that of *S. americanus*. The mean durations of the first four stages at 24 ± 1°C were between 5.8 and 6.8 days; the total duration through stage VI was 44 days. Complete larval development at 25°C therefore probably requires about six weeks. The seasonal occurrence of phyllosomas collected in plankton indicates that some spawning may take place throughout most of the year.

4. *Scyllarus* n. sp. Ovigerous females of an undescribed species of *Scyllarus* were collected by R/V JOHN ELLIOTT PILLSBURY in the extreme southwestern Caribbean Sea. Larvae were hatched in the laboratory and reared to a late stage of development in stage VI. Planktonic specimens were not available for comparison. It appears that the larval history would consist of seven phyllosoma stages, although growth may have been somewhat retarded. Phyllosomas of *Scyllarus* n. sp. closely resemble those of *S. chacei*. Stage I differs from the latter by the slightly smaller total length, by the possession of only six pairs of natatory setae on the exopod of pereiopod 2, and in some individuals by the possession of five apical setae on maxilla 2. In later stages the length of the eye and stalk relative to the antennule may be slightly greater than in *S. chacei*. The mean durations of the

first four stages at 25°C were between 5.2 and 6.2 days; the total duration through stage V was about 30 days. The length of larval life therefore is probably comparable to that of *S. chacei*.

5. *Scyllarides aequinoctialis*. Larvae hatched in the laboratory in a free-swimming naupliosoma stage, which within a few minutes molted to the first phyllosoma. The phyllosomas were reared with progressive morphological development to stage VIII (TL about 6 mm). The most advanced stage reared was linked with a sequence of later larvae, up to length 28.8 mm, collected in plankton. The planktonic specimens did not fall into well defined "stages" in either length or morphology. The last two stages have been described by Sims (1964), and were later reported by Sims (1965a) as stages 11 and 12 of *Parribacus* sp. It is clear that most larvae previously attributed to *Scyllarides* have been erroneously identified and belong in reality to various species of *Scyllarus*. A diagnosis of the larvae of *Scyllarides aequinoctialis* is as follows: Stage I 1.9 mm in length, with biramous antenna, pear-shaped fore-body, pereiopod 3 1.3 times length of pereiopod 2, excluding dactyl; exopod of pereiopods 1-2 with six pairs of natatory setae. Early stages similar to other species of *Scyllarides* and related genera. Pereiopod 5 becoming well developed, with setose exopod, at relatively early stage. Phyllosoma identifiable by TL 6-7 mm with fore-body slightly wider than hind-body, eyestalk/antennule ratio 1.2-1.4, inner ramus of antenna with

articulation, outer ramus a short triangular process. Antenna with remnant of exopod up to TL 21-22 mm, then with lateral process. Fore-body becoming progressively broader anteriorly and increasingly wider than hind-body, in later stages semielliptical in outline. Length of final stage 36-41 mm. The total duration through the first eight stages reared at 24 ± 1°C was 94 days. Complete larval development undoubtedly requires several, perhaps eight or nine, months.

6. Scyllarides nodifer. A sequence of representative phyllosoma stages collected in plankton, ranging from 6.6 mm in length to the final phyllosoma (TL 36.7 mm), is described. These larvae differ from those of Scyllarides aequinoctialis primarily in that pereiopod 5 remains rudimentary throughout development, and in the form of the dactyl of pereiopod 4. There are slight differences in the proportions of the fore-body. The phyllosomas appear to belong to the same species as stages 4-10 of the sequence attributed by Sims (1965a) to Parribacus. A considerable body of evidence now indicates that they belong instead to Scyllarides nodifer. The seasonal distribution of phyllosomas and postlarvae believed to be S. nodifer suggests a larval life of six to ten months. The phyllosomas from the Mediterranean Sea assigned to Thenus by Stephensen (1923) and Santucci (1926) are regarded as larvae of Scyllarides latus.

7. Parribacus antarcticus. Phyllosomas 8.5, 13, 24 and 65 mm in length, collected in plankton in the western Atlantic, are described. The largest specimen represents the

subfinal stage and is similar to a larva from the Indian Ocean reported as "*Parribacus* β " by Saisho (1966b). The specimen 36.5 mm in length from the Straits of Florida designated "Phyllosome D" by Sims (1964), belongs to the same species as the larvae described herein. Available evidence indicates that phyllosomas of this form belong to *Parribacus*, as Gurney (1936) suggested. Early stages resemble *Scyllarides*. Pereiopod 5 becomes well developed, with a setose exopod, at a relatively early stage as in *S. aequinoctialis*. The form of the antenna in the 8.5-mm phyllosoma helps bridge the gap between the biramous antenna of the early stages of *Parribacus antarcticus*, described by Saisho (1962b, 1966b), and later stages from the plankton. The antenna by TL about 9 mm loses the exopod, and is uniramous in subsequent stages up to TL 36 mm, when the lateral process begins to become differentiated. The fore-body, which is pear-shaped in early stages, becomes progressively broader anteriorly. The final phyllosoma attains a length of 75-80 mm. Postlarvae are 50 mm or more in total length. The duration of the earliest stages, reported by Saisho, is comparable to that of *S. aequinoctialis*. There is no basis for estimating the duration of larval life other than the large size attained and the probable large number of stages; they suggest a relatively long duration.

8. ?*Arctides guineensis*. A sequence of representative phyllosoma stages collected in plankton, ranging from 6.6 mm in length to the final stage (TL 59.2 mm), is described.

The larvae resemble those of *Scyllarides aequinoctialis* but differ markedly in certain features. The eyestalk/antennule ratio is greater and the fore-body after the early stages becomes much narrower than the hind-body. The dactyls of pereiopods 4 and 5 are short and essentially identical. The development of the antenna parallels that of *Scyllarides*. There is no spiniform process in the last stages at the mid-line of the posterodorsal margin of abdominal segments 4 and 5. The geographic distribution of the phyllosomas, off the Atlantic coast of Florida and between the northern Bahamas and Bermuda, is consistent with that of the adult of *Arctides*. In view of this and the close relationship between adults of *Scyllarides* and *Arctides*, the larvae are provisionally referred to *A. guineensis*. The larval life, as in *Scyllarides* and *Parribacus*, is no doubt relatively long.

9. Phyllosoma Q. One specimen, 10.8 mm in length, from the Straits of Florida is described and illustrated. The phyllosoma possesses a unique combination of characters. The abdomen, antenna and maxilla 2 are characteristic of larvae of *Scyllarus*, whereas the well developed pereiopod 5 with setose exopod, the shape and proportions of the fore-body and the length of the eyestalk correspond to the *Scyllarides aequinoctialis*-*Parribacus* type of phyllosoma. This larva may belong to *Scyllarus faxoni*, the most primitive western Atlantic representative of the genus, or to an undiscovered scyllarid lobster.

10. Starved stage I phyllosomas did not molt. Larvae

of the species reared can develop at 20°C, with a longer duration than at 25°C. The duration of the stages at 30°C was somewhat shorter than at 25°C, but mortality was high. Molting is severely inhibited or prevented entirely at 15°C.

11. The genus *Scyllarus* in general has a comparatively short larval life, ranging among different species from about one to three or four months. The number of stages ranges from a minimum of about six to ten or more.

12. Many other scyllarid lobsters appear to have a larval life as long as, if not longer than, that of *Panulirus*, and a relatively large number of stages which are difficult to define.

13. The presence or absence of a setose exopod on maxilliped 3 among larvae of the Palinuridae supports the view of George and Main (1967) of the early divergence of the Palinuridae into a stridulating line (Stridentes) and a nonstridulating line (Silentes).

14. The absence of a setose exopod on maxilliped 3 in larvae of *Jasus* (Silentes) and all Scyllaridae, as well as the close resemblance between the stage I phyllosomas of *Jasus*, *Parribacus* and *Scyllarides*, are considered evidence for the derivation of the Silentes and the Scyllaridae from a common ancestor, supporting Boas' interpretation of adult homologies.

15. Later larvae of *Jasus* differ from those of all known Scyllaridae and agree with those of all known Stridentes in the possession of setae on the exopod of maxilla 2 and in the length and form of the antenna.

16. The first larval stage of *Palinurellus* as described by Sims (1966a) is a primitive palinurid phyllosoma, with a setose exopod on maxilliped 3. *Palinurellus* apparently represents the earliest living offshoot of the nonstridulating stock which later gave rise on the one hand to the Stridentes, and on the other to the Silentes and the Scyllaridae.

17. It may be inferred, from the larval characters of *Palinurellus*, that the larva of the ancestral scyllaridean possessed a setose exopod on maxilliped 3 and a biramous antenna at hatching, and that later stages possessed: (1) a cephalic shield which covered the entire thorax; (2) a well developed pereiopod 5, with setose exopod; and (3) setae on the exopod of maxilla 2. The divergence of the Silentes from the ancestral form was accompanied in the larva by the loss of the exopod of maxilliped 3. The divergence of the Scyllaridae from the early Silentes line was further accompanied in the larva by the loss of the setae of maxilla 2 and by the evolution of the characteristic scyllarid antennal form.

18. In addition to *Palinurellus*, larvae of *Ibacus* among the Scyllaridae and of ?*Puerulus* among the Stridentes have retained, with modifications, the primitive condition of the cephalic shield.

19. Larvae of the more primitive genera of both families (*Palinurellus*, ?*Puerulus*, *Jasus*, *Ibacus*, *Scyllarides*, *Parribacus*, ?*Arctides*) retain the biramous antenna at hatching. The antenna is uniramous in larvae of the more highly evolved

genera of both families (*Palinurus*, ?*Justitia*, *Panulirus*, *Thenus*, *Scyllarus*).

20. Larvae of the most primitive palinurids (*Palinurellus*, ?*Puerulus*) and the more primitive scyllarids retain the primitive condition of pereiopod 5. In larvae of most palinurids and in *Thenus*, *Scyllarus* and some species of *Scyllarides*, the development of pereiopod 5 is suppressed.

21. The degree of development of pereiopod 5 among larvae of *Scyllarides* indicates the existence of two species groups within the genus, apparently at different levels of evolution. In the more primitive, represented by *S. aequinoctialis*, pereiopod 5 becomes well developed at a relatively early stage. In the more advanced group, including *S. nodifer*, *latus*, and probably *herklotsii* and *delfosi*, it remains rudimentary.

22. Larval characters indicate that *Parribacus* has a closer phylogenetic affinity with *Scyllarides* than with *Ibacus*, despite the superficial resemblance of adults of *Parribacus* to the latter.

23. Larval characters agree with adult structure in indicating that *Scyllarus*, in an evolutionary sense, is well separated from other Scyllaridae, and has no close relationship with *Scyllarides*. Phyllosoma Q, by its unique combination of characters, appears to represent a phylogenetic link between phyllosomas of the more primitive scyllarids and those of *Scyllarus*.

24. Existing techniques have proven unsatisfactory for rearing

larvae of most Scyllaridea through their complete development in the laboratory. Brine shrimp nauplii are believed to be an inadequate food for later phyllosomas of most species. Further studies on the feeding of phyllosoma larvae are needed.

PART VIII

FIGURES

Figure 1

Schematic drawing of a phyllosoma larva in ventral view.

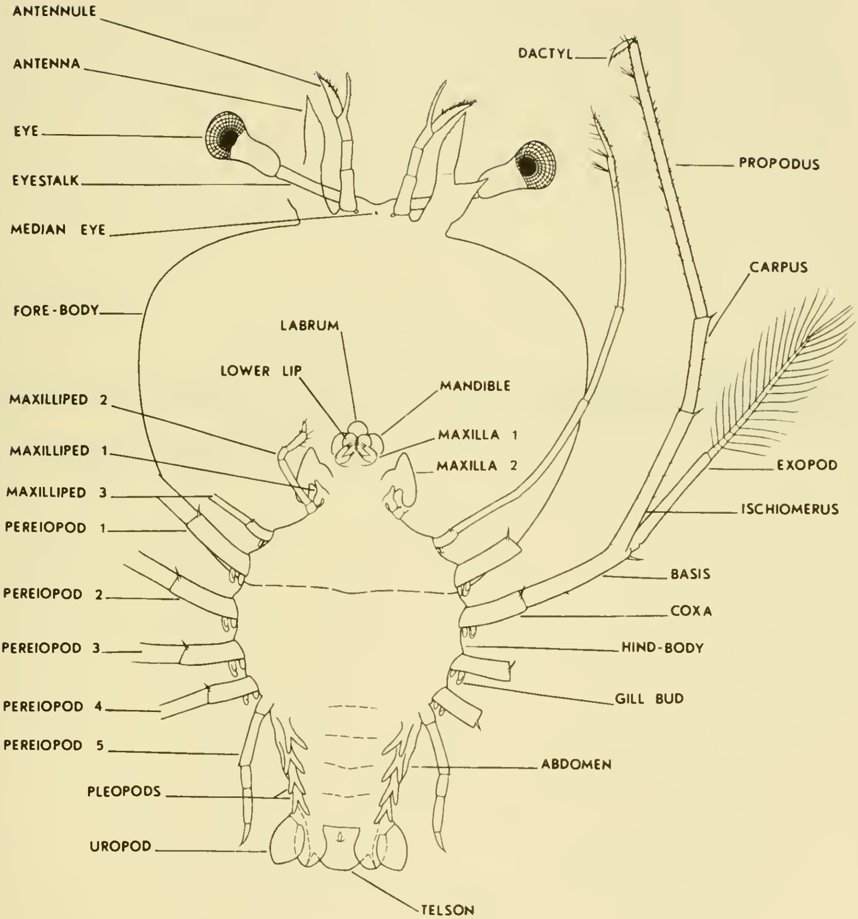

ANTENNULE
ANTENNA
EYE
EYESTALK
MEDIAN EYE
FORE-BODY
MAXILLIPED 2
MAXILLIPED 1
MAXILLIPED 3
PEREIOPOD 1
PEREIOPOD 2
PEREIOPOD 3
PEREIOPOD 4
PEREIOPOD 5
PLEOPODS
UROPOD
DACTYL
PROPODUS
CARPUS
LABRUM
LOWER LIP
MANDIBLE
MAXILLA 1
MAXILLA 2
EXOPOD
ISCHIOMERUS
BASIS
COXA
HIND-BODY
GILL BUD
ABDOMEN
TELSON

Figure 2

Survival of starved stage I larvae of *Scyllarus americanus* at various temperatures.

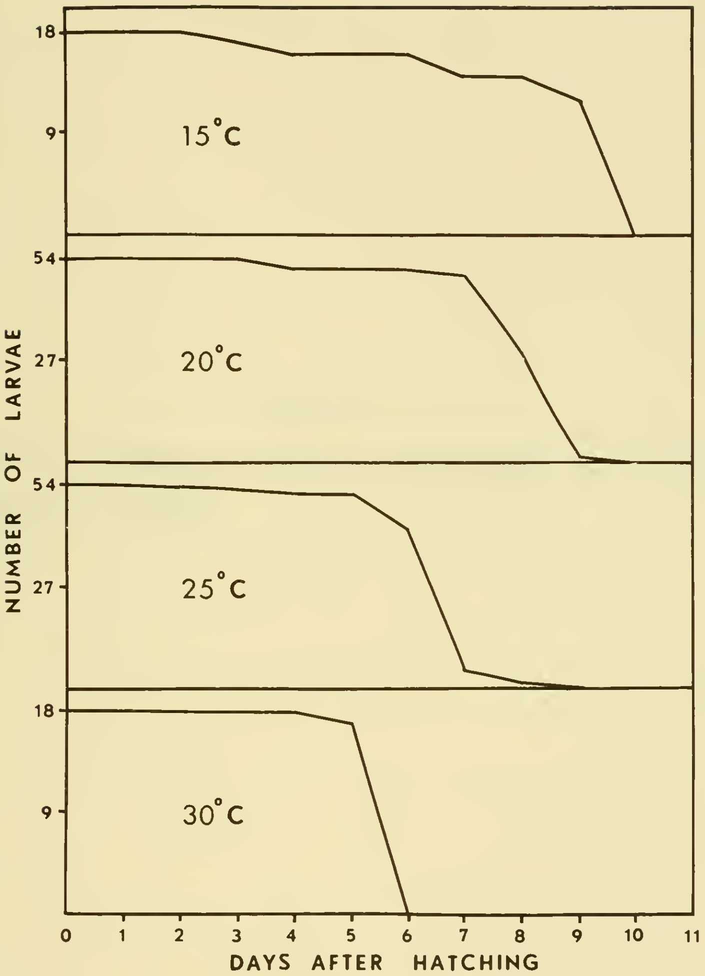

18
9
15°C
54
27
20°C
54
27
25°C
18
9
30°C
NUMBER OF LARVAE
0
1
2
3
4
5
6
7
8
9
10
11
DAYS AFTER HATCHING

Figure 3

Larval development of *Scyllarus americanus* in various salinities at 25°C.

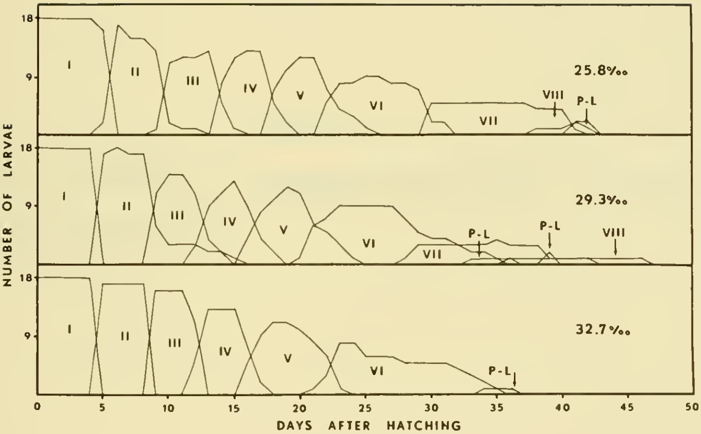

18
9
18
9
18
9
NUMBER OF LARVAE
I
II
III
IV
V
VI
VII
VIII
P-L
25.8‰
I
II
III
IV
V
VI
VII
P-L
P-L
VIII
29.3‰
I
II
III
IV
V
VI
P-L
32.7‰
0
5
10
15
20
25
30
35
40
45
50
DAYS AFTER HATCHING

Figure 4

Larval development of *Scyllarus americanus* in various salinities at 20°C.

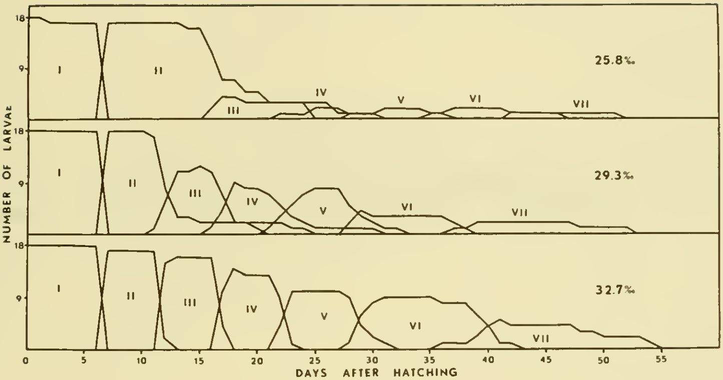

18
9
I
II
III
IV
V
VI
VII
25.8‰
29.3‰
32.7‰
NUMBER OF LARVAE
0
5
10
15
20
25
30
35
40
45
50
55
DAYS AFTER HATCHING

Figure 5

Larval development of Scyllarus americanus at various temperatures; salinity range 35.6 to 38.6 °/oo.

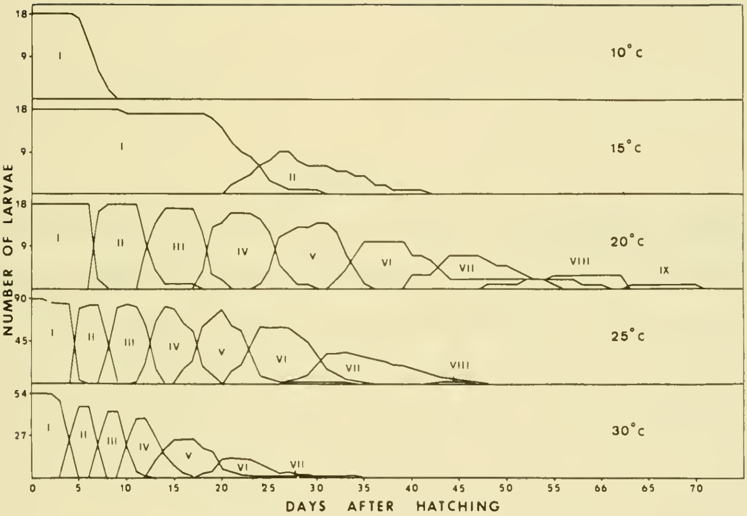

18
9
I
10°c
18
9
I
II
15°c
18
9
I
II
III
IV
V
VI
VII
VIII
IX
20°c
90
45
I
II
III
IV
V
VI
VII
VIII
25°c
54
27
I
II
III
IV
V
VI
VII
30°c
NUMBER OF LARVAE
0
5
10
15
20
25
30
35
40
45
50
55
66
65
70
DAYS AFTER HATCHING

Figure 6

Mean duration of the larval stages of _Scyllarus americanus_ reared under various conditions. Solid line represents five individuals that produced postlarvae from stage VI in various salinities at 25°C. Dashed 25° line represents four individuals in various salinities that produced postlarvae from stage VII. Irregularly broken 25° line represents larvae at salinity 35.6-38.6 °/oo which did not metamorphose.

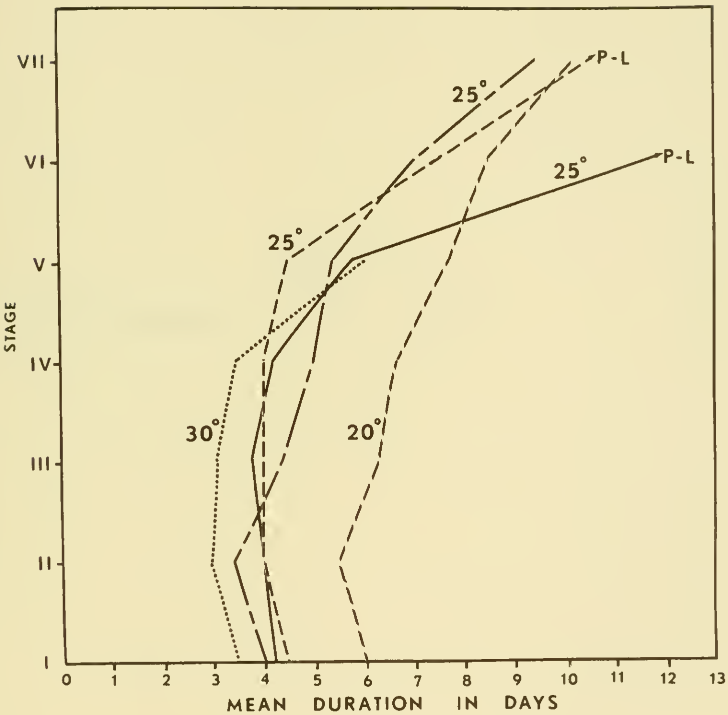

VII
VI
V
IV
III
II
I
STAGE
0
1
2
3
4
5
6
7
8
9
10
11
12
13
MEAN DURATION IN DAYS
25°
P-L
25°
P-L
25°
30°
20°

Figure 7

Scyllarus americanus. Stage I, reared.

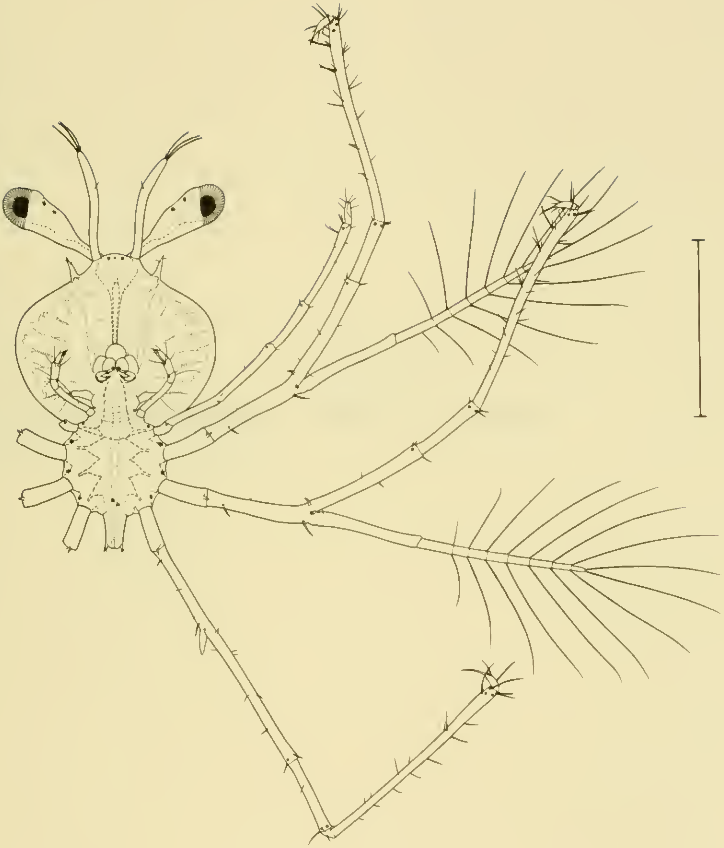


Figure 8

Scyllarus *americanus*. Stage II, reared.

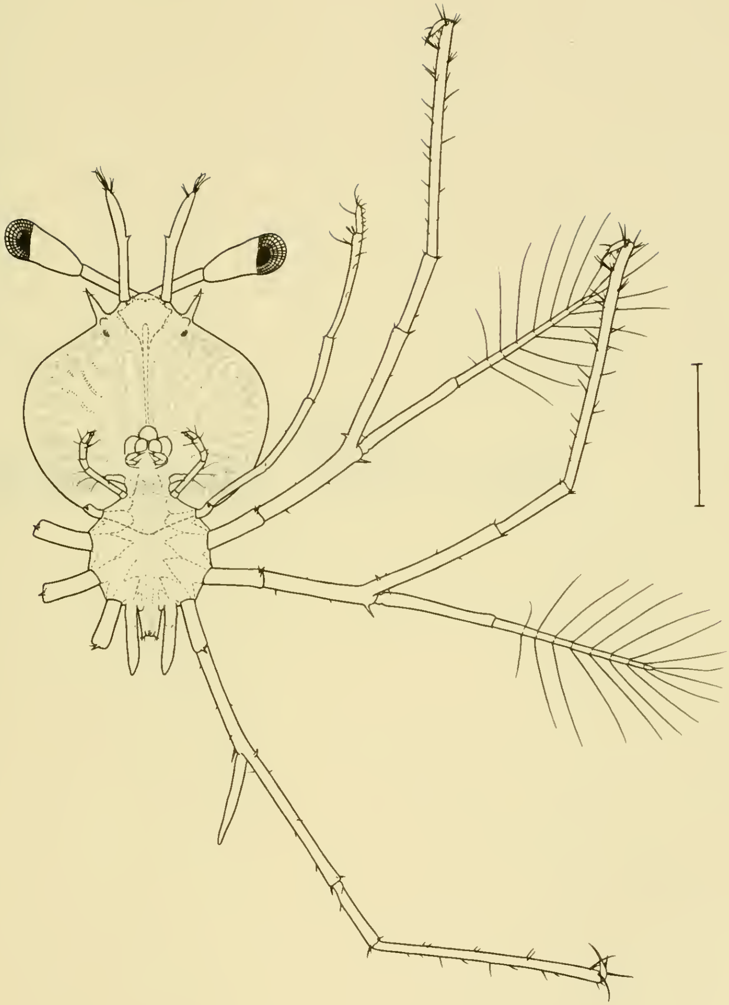


Figure 9

Scyllarus americanus. Stage III, reared.

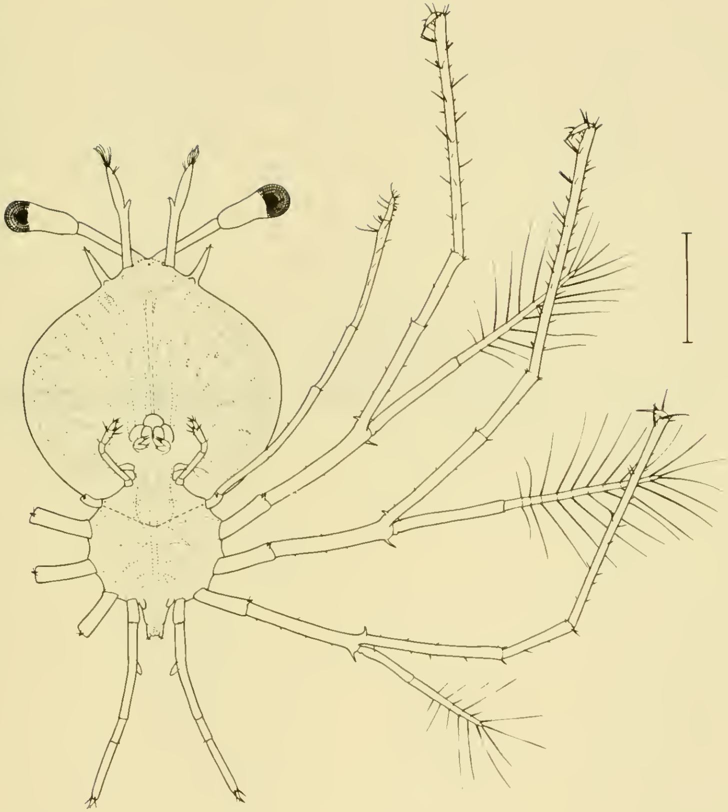


Figure 10

Scyllarus americanus. Stage IV, reared.

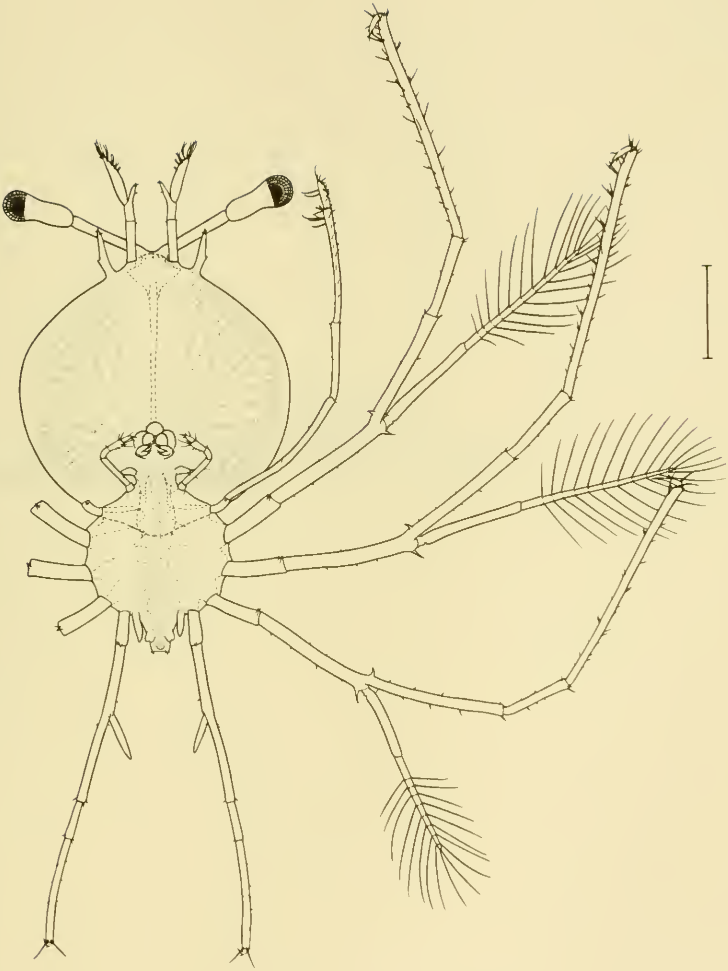


Figure 11

Scyllarus americanus. Stage V, reared.

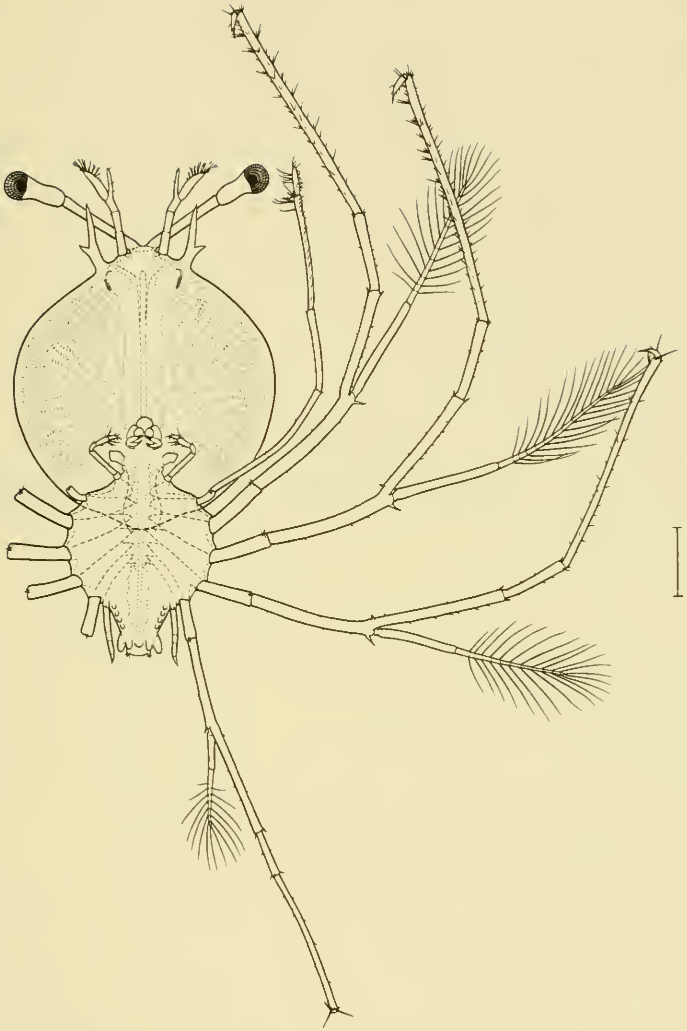


Figure 12

Scyllarus americanus. Stage VI, reared.

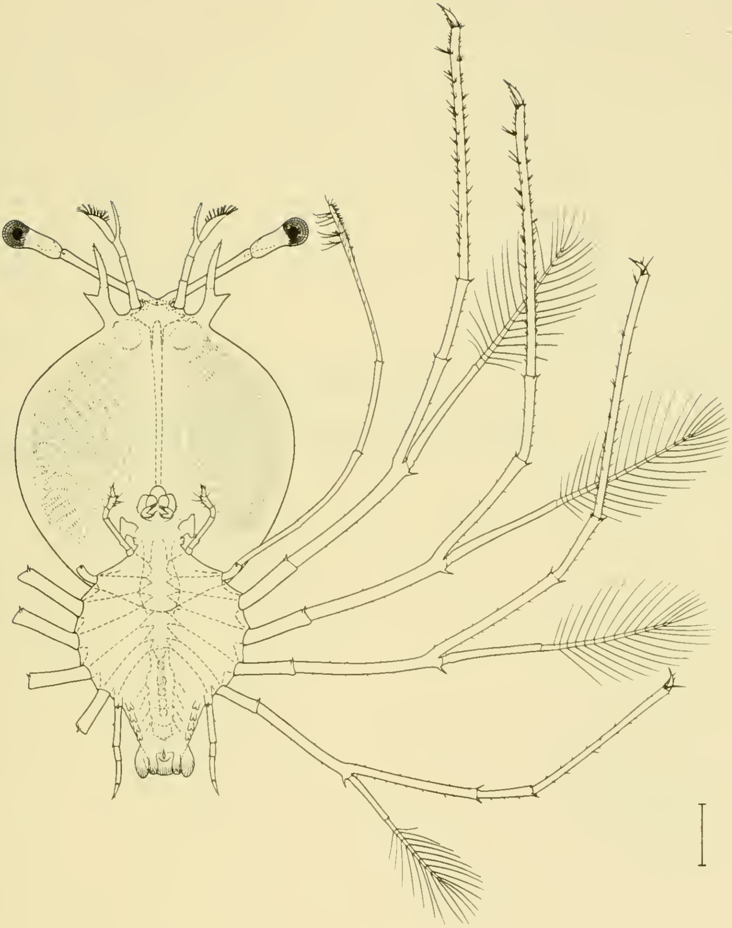


Figure 13

Scyllarus americanus. Stage VII, reared.

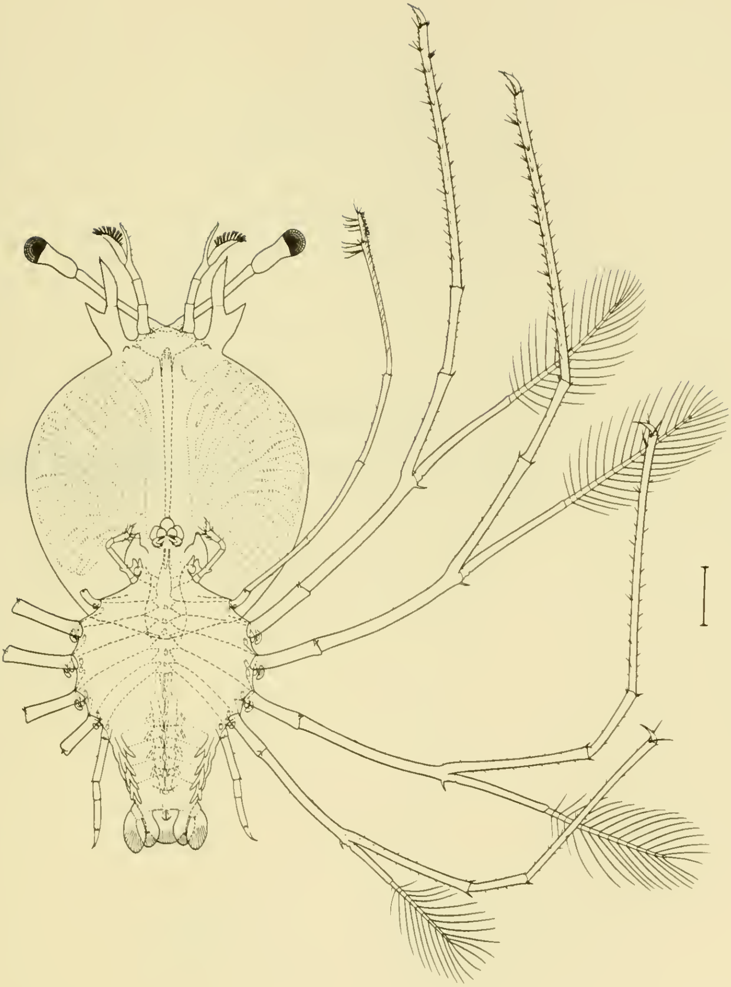


Figure 14

Scyllarus americanus. Postlarva, reared.

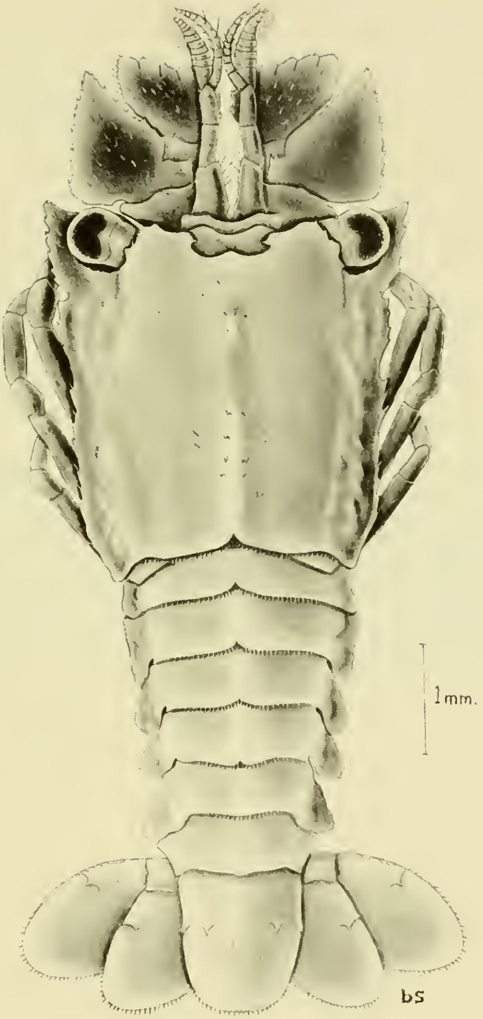

1mm.
bs

Figure 15

Scyllarus americanus. Postlarva, reared. A, semidiagrammatic lateral view. Appendages posterior to the antennae are omitted. Arrows indicate the absence of distinct spines. B, left pleopod of 2nd abdominal segment. Setules are omitted.

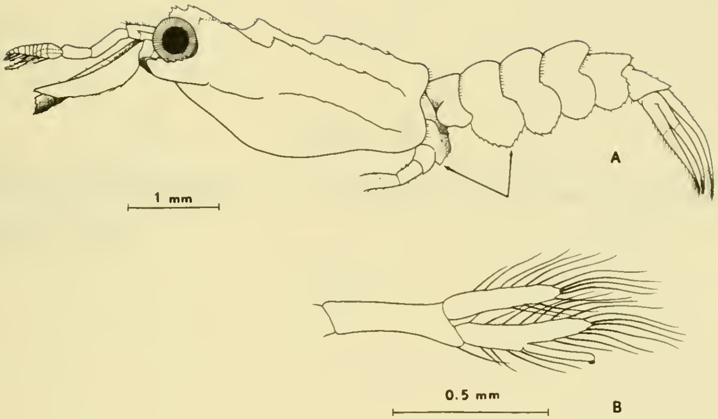

A
1 mm
0.5 mm
B

Figure 16

Scyllarus americanus. Antennule and antenna of phyllosoma stages I-VII.

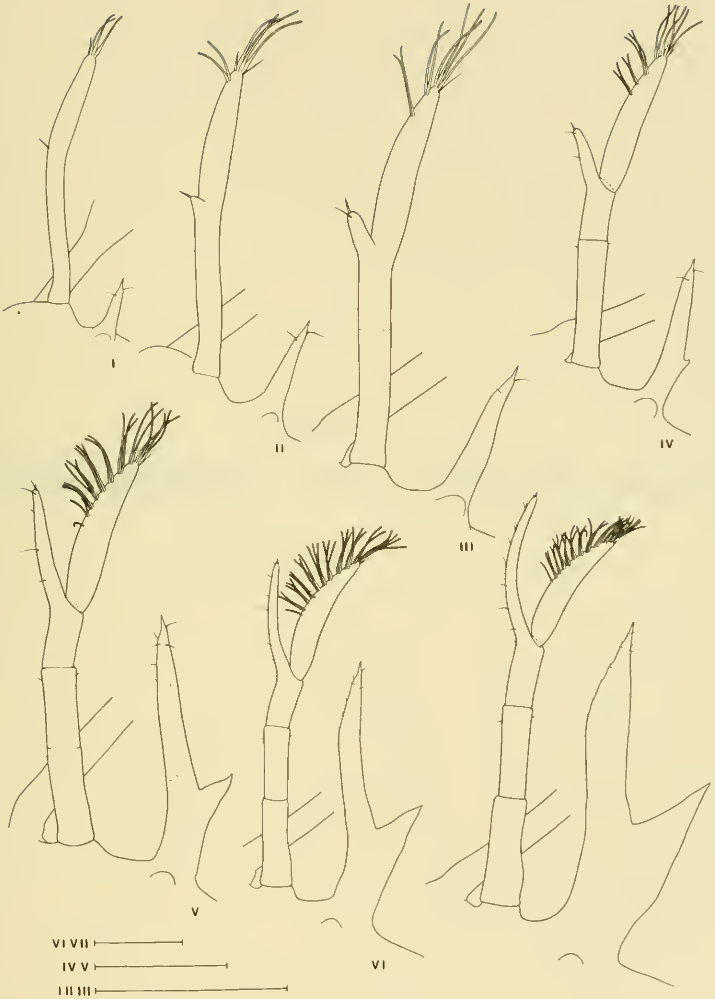

I
II
III
IV
V
VI
VI VII
IV V
I II III

Figure 17

Scyllarus *americanus*. Abdomen of phyllosoma stages I-VII.

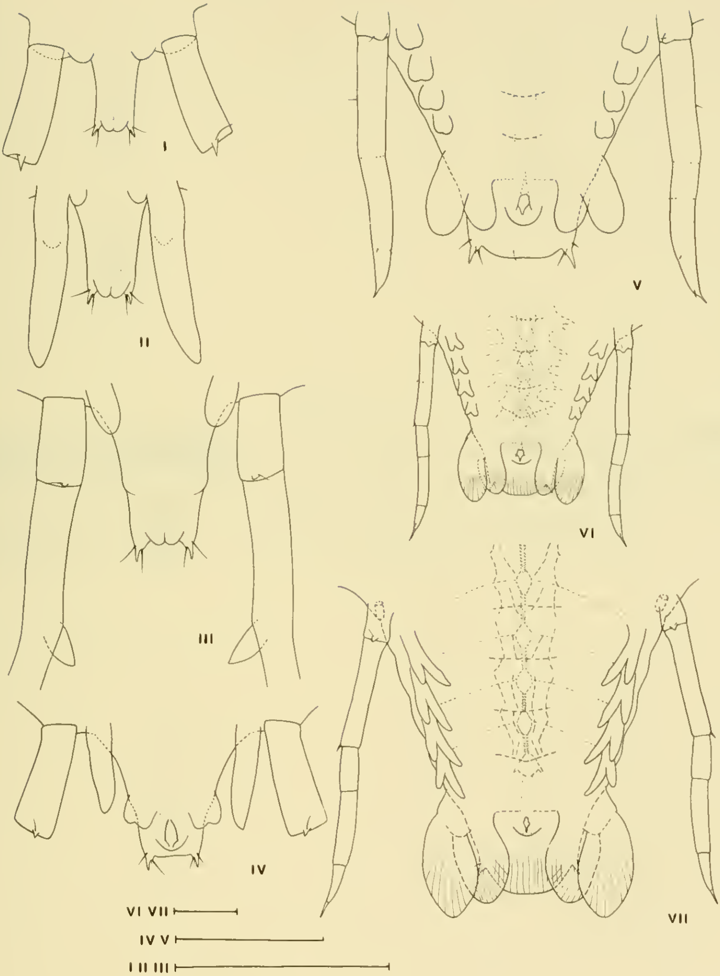

I
II
III
IV
V
VI
VII
VI VII
IV V
I II III

Figure 18

Scyllarus americanus. Mouthparts of phyllosoma stages. I-VII, maxilla 2 and maxilliped 1 of stages I-VII. A, left mandible, stage I. B, left mandible, stage VII.

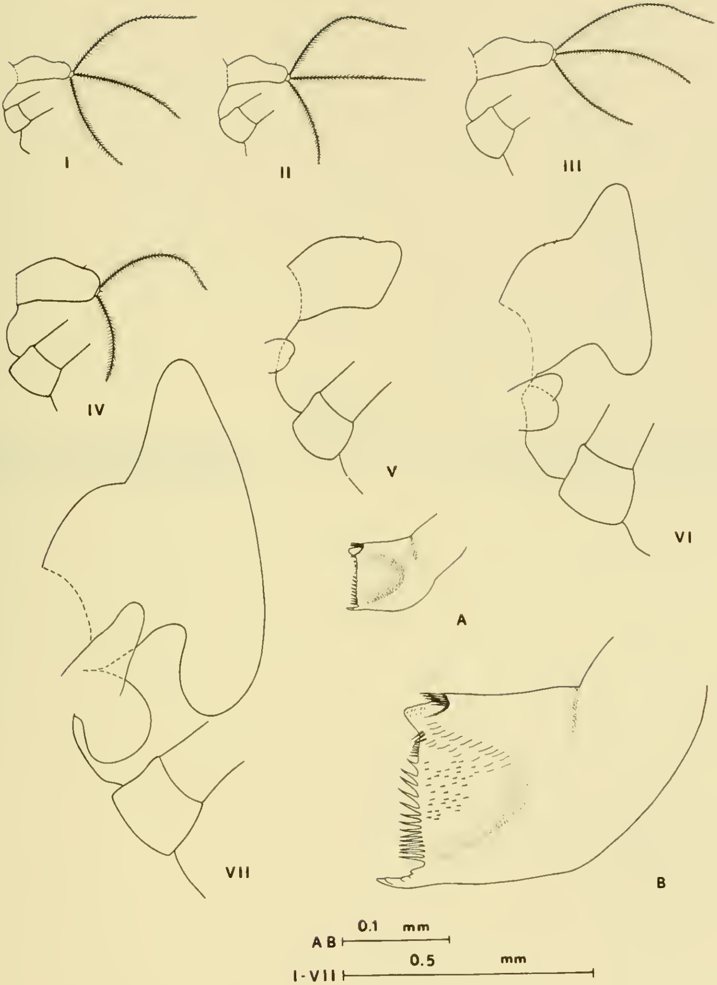
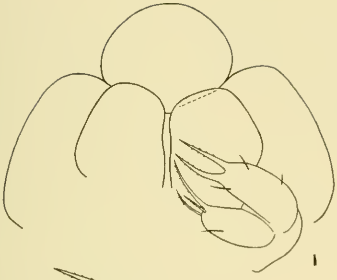
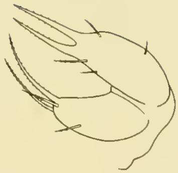

I
II
III
IV
V
VI
VII
A
B
A B
0.1 mm
I - VII
0.5 mm

Figure 19

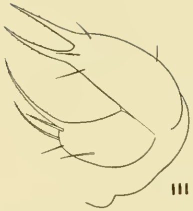
Scyllarus americanus. Maxilla 1 of phyllosoma stages I-VII.



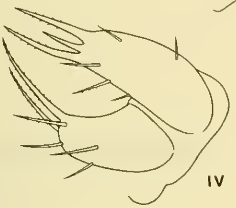
I



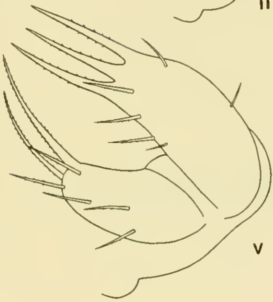
II



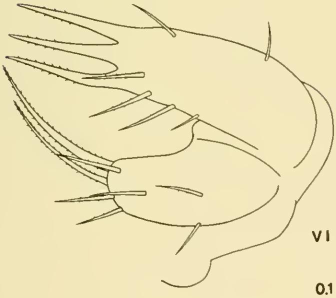
III



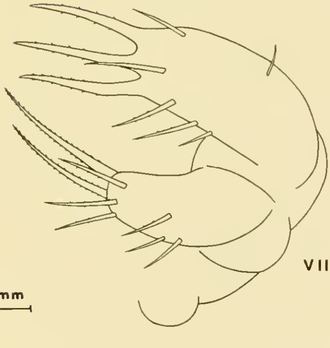
IV



V



VI



VII

0.1 mm

Figure 20

Scyllarus americanus. Maxilliped 2 of phyllosoma stages I-VII.

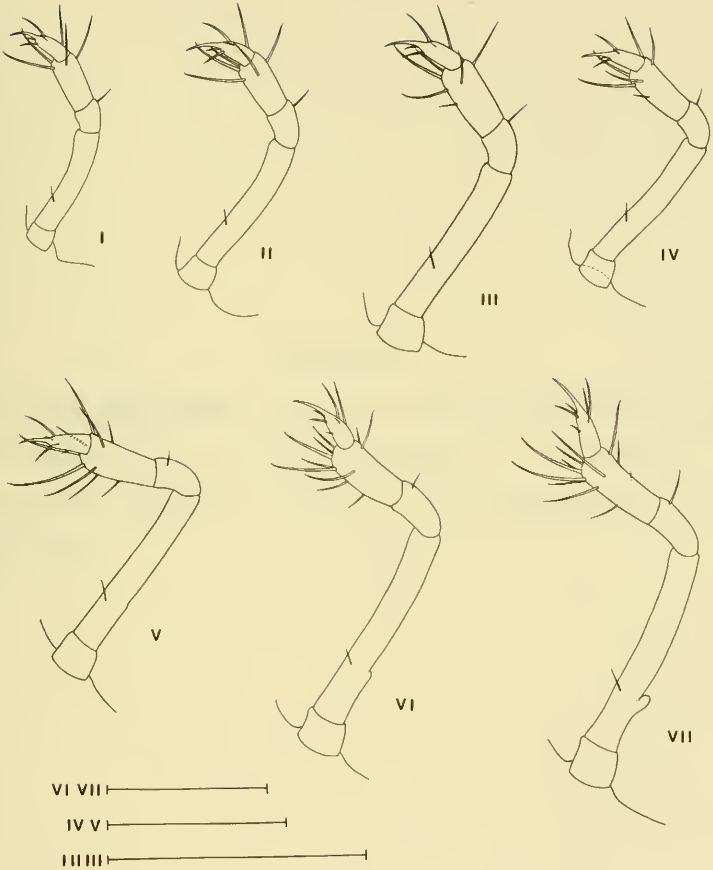

I
II
III
IV
V
VI
VII
VI VII
IV V
I II III

Figure 21

Scyllarus americanus. Distal end of pereiopods of phyllosoma stages. A, B, C: pereiopods 1, 2, 3, stage I. D, pereiopod 4, stage IV. E, F, G, H: pereiopods 1, 2, 3, 4, stage VII.

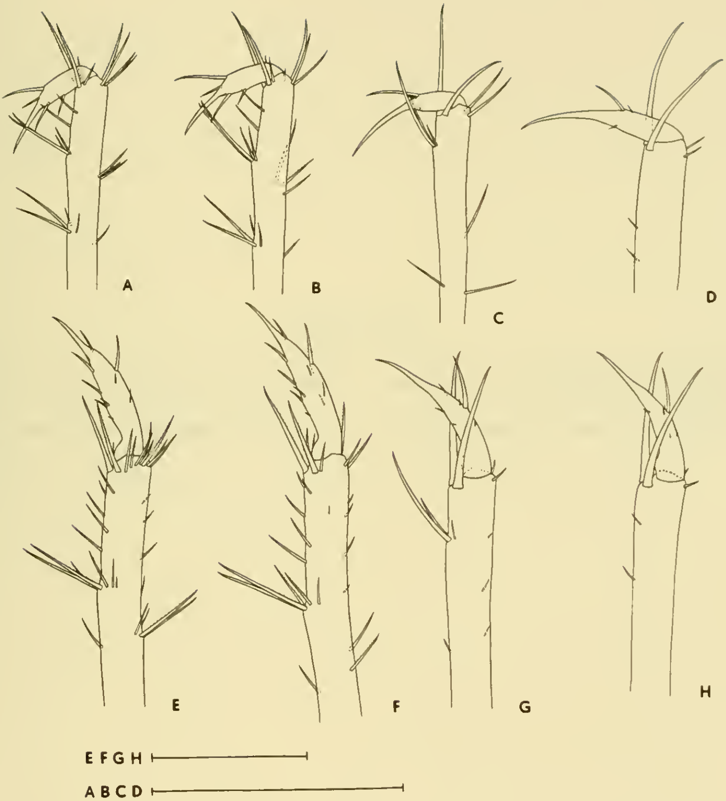

A
B
C
D
E
F
G
H
E F G H
A B C D

Figure 22

Survival of starved stage I larvae of *Scyllarus nearctus* at various temperatures. o indicates 50 per cent mortality.

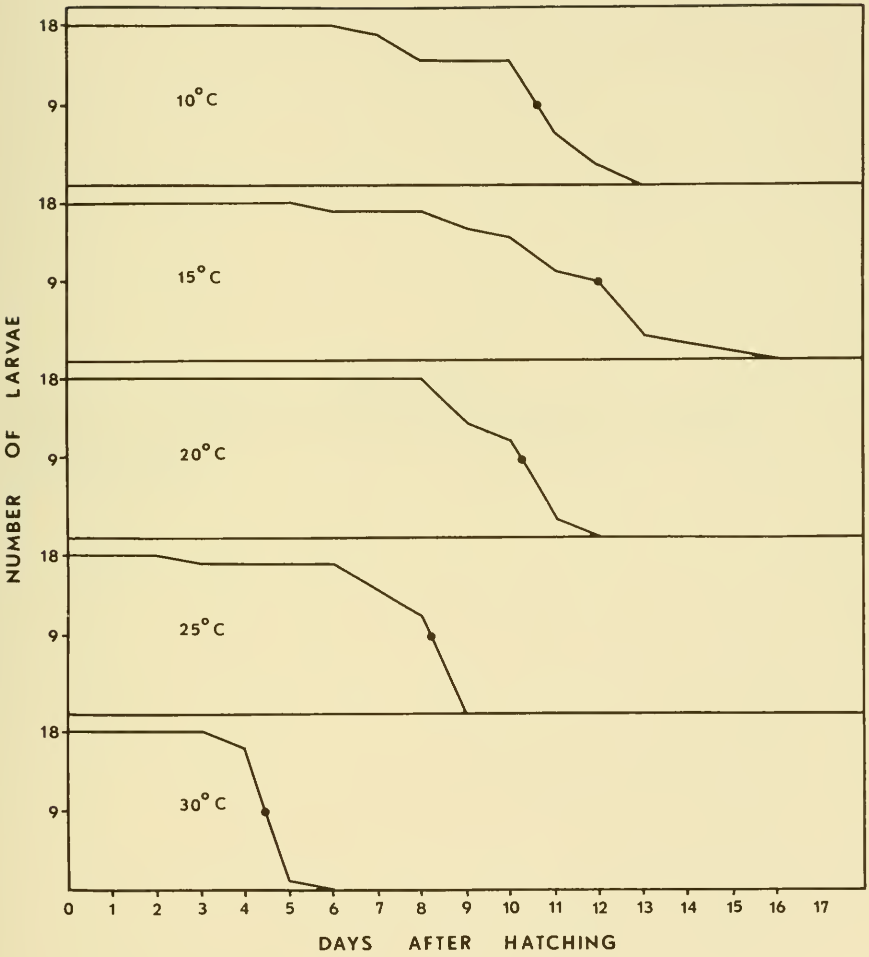

18
9
10° C
15° C
20° C
25° C
30° C
NUMBER OF LARVAE
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
DAYS AFTER HATCHING

Figure 23

Larval development of *Scyllarus nearctus* at various temperatures.

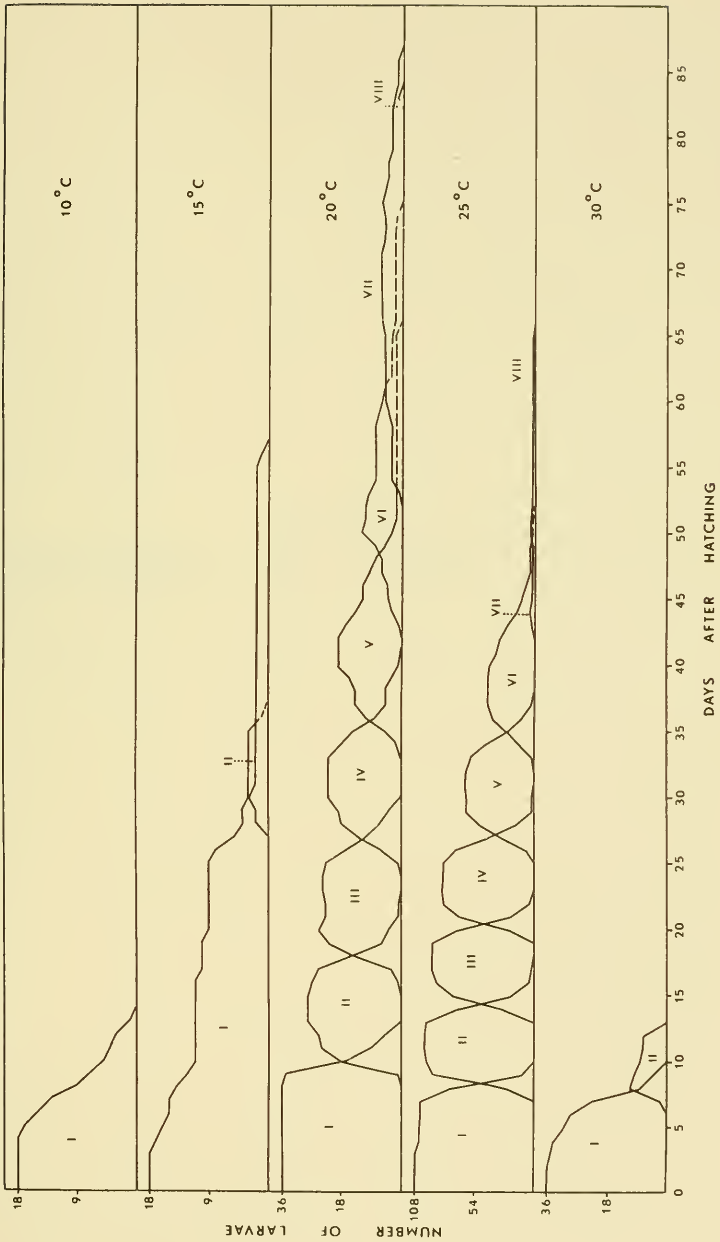

10 °C
15 °C
20 °C
25 °C
30 °C
I
I
II
I
II
III
IV
V
VI
VII
VIII
I
II
III
IV
V
VI
VII
VIII
I
II
18
9
18
9
36
18
108
54
36
18
NUMBER OF LARVAE
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
85
DAYS AFTER HATCHING

Figure 24

Scyllarus nearctus. Stage I, reared.

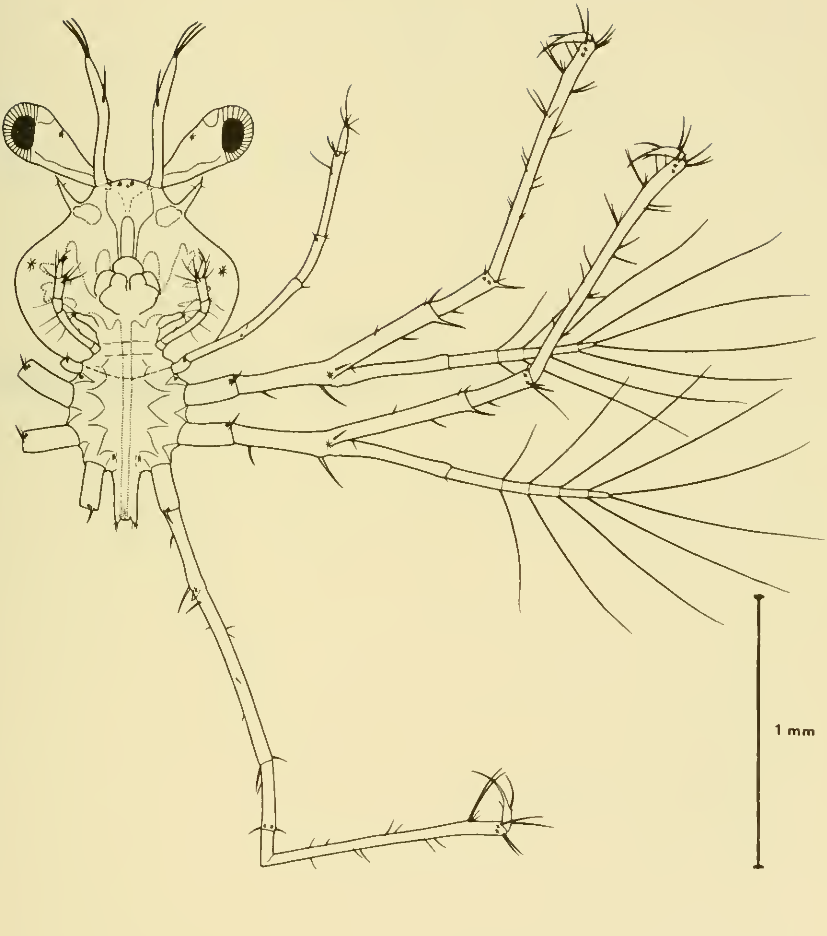

1 mm

Figure 25

Scyllarus nearctus. Stage II, reared.

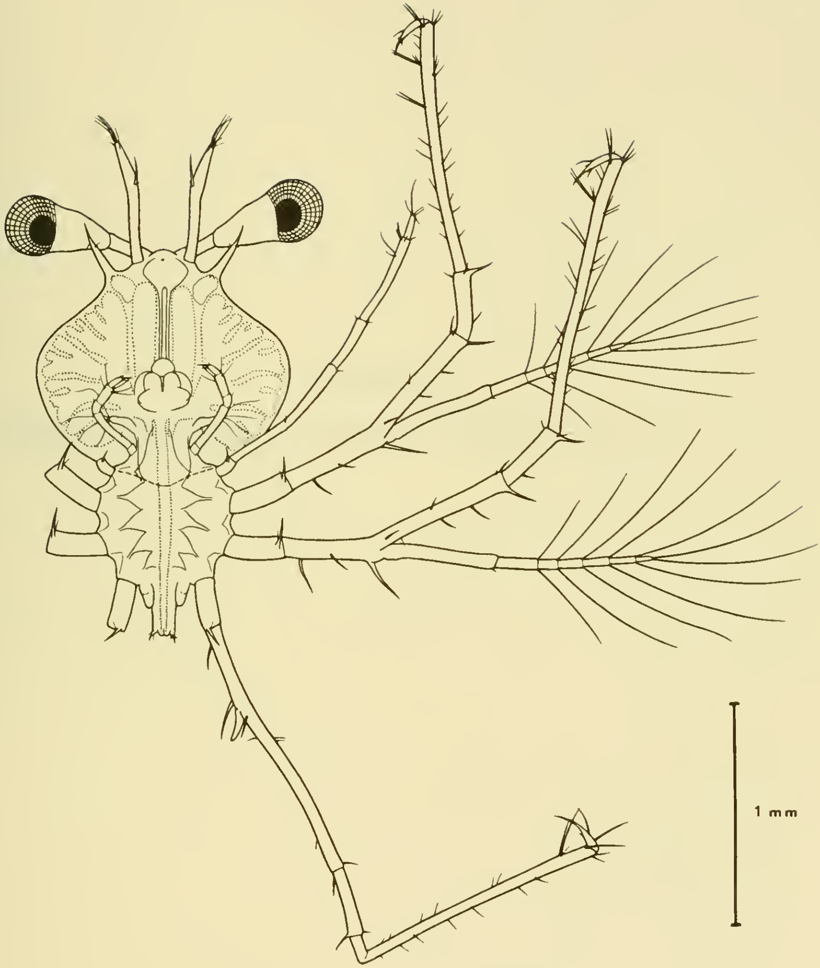

1 mm

Figure 26

Scyllarus nearctus. Stage III, reared.

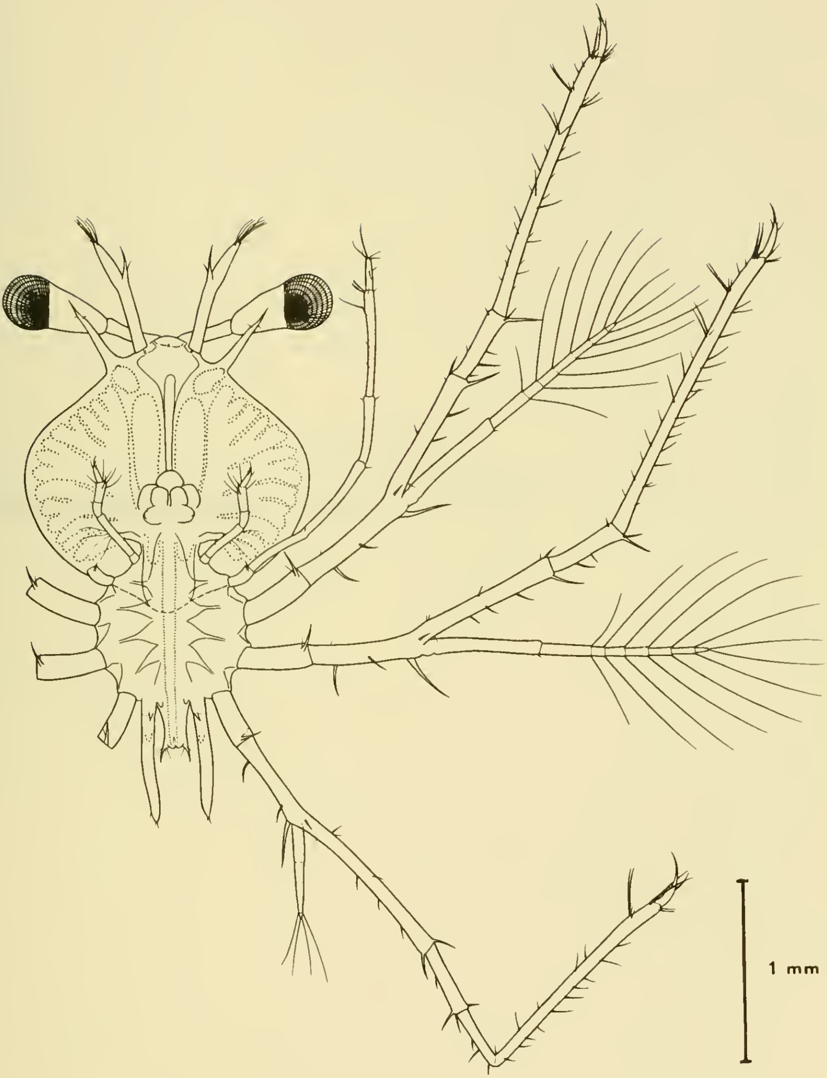

1 mm

Figure 27

Scyllarus nearctus. Stage IV, reared.

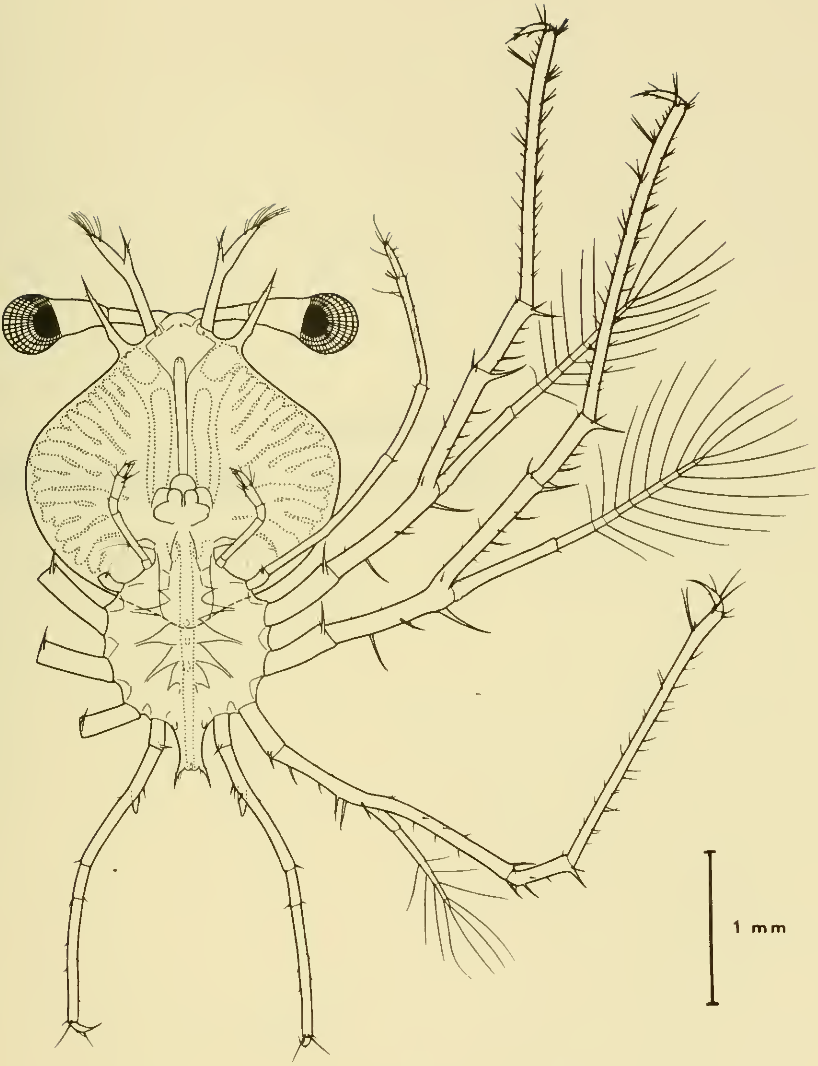

1 mm

Figure 28

Scyllarus nearctus. Stage V, reared.

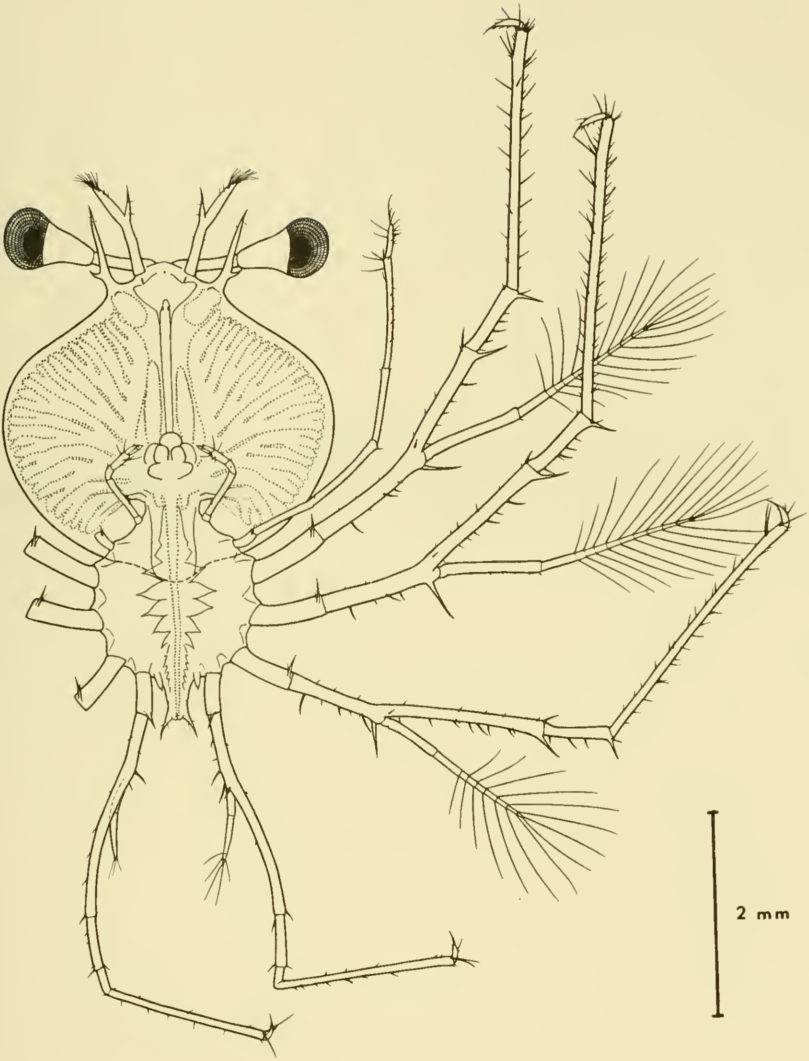

2 mm

Figure 29

Scyllarus nearctus. Stage VI, reared.

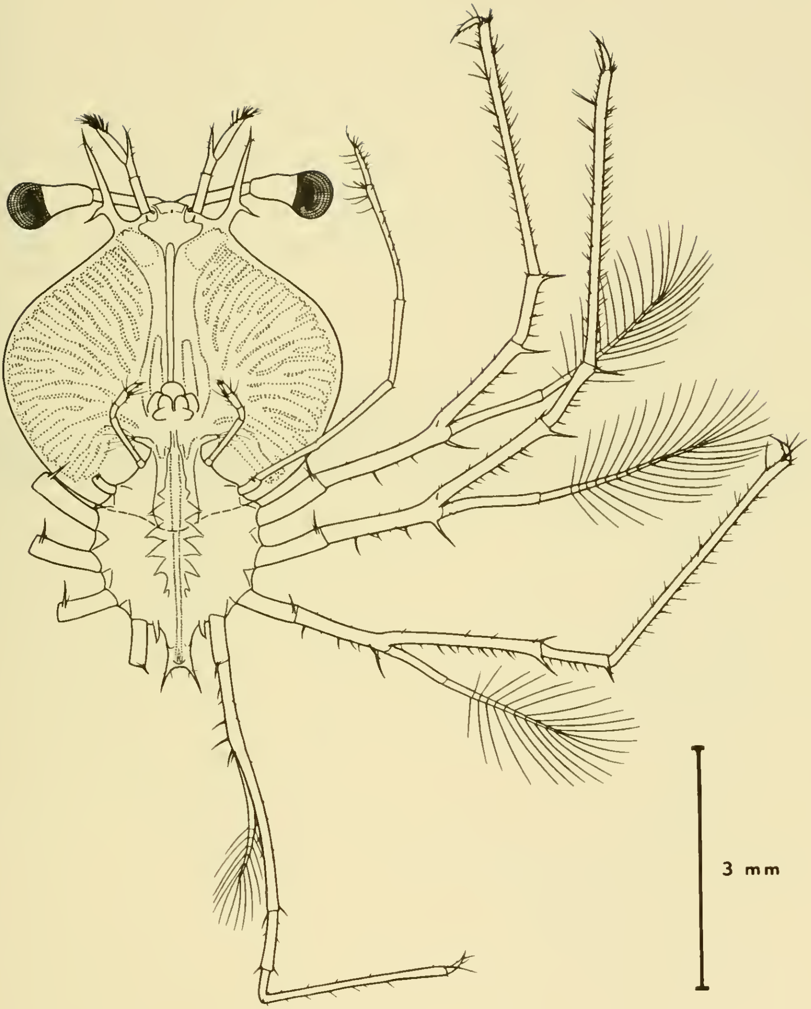

3 mm

Figure 30

Scyllarus nearctus. Stage VII, reared.

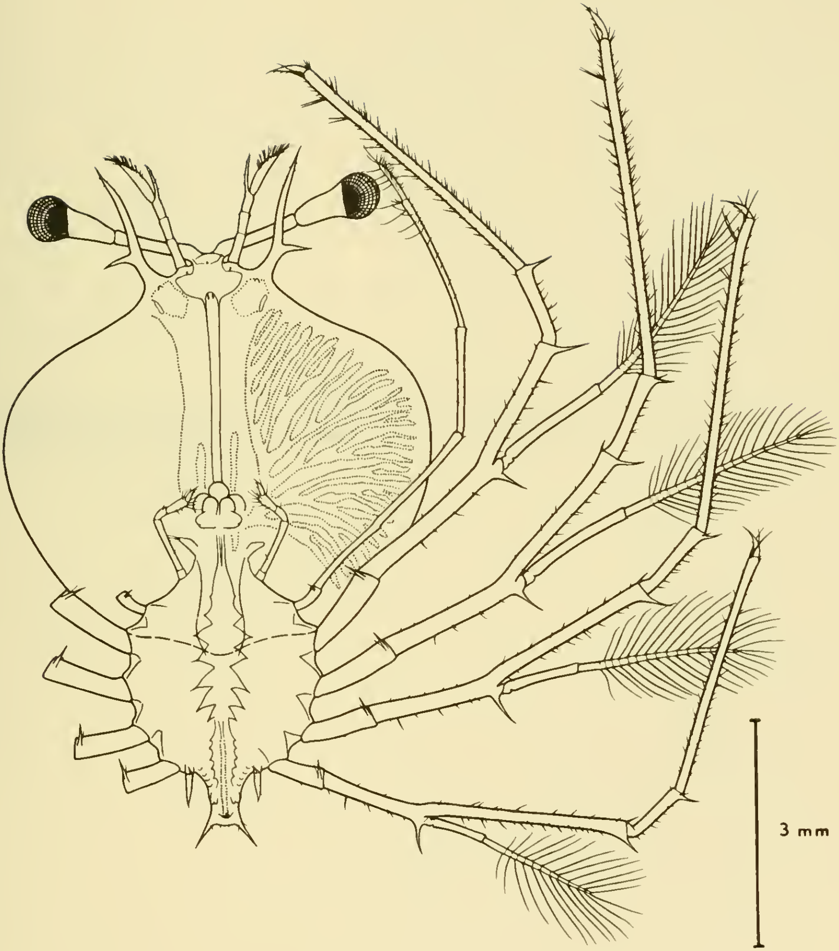

3 mm

Figure 31

Scyllarus nearctus. Stage VIII, plankton.

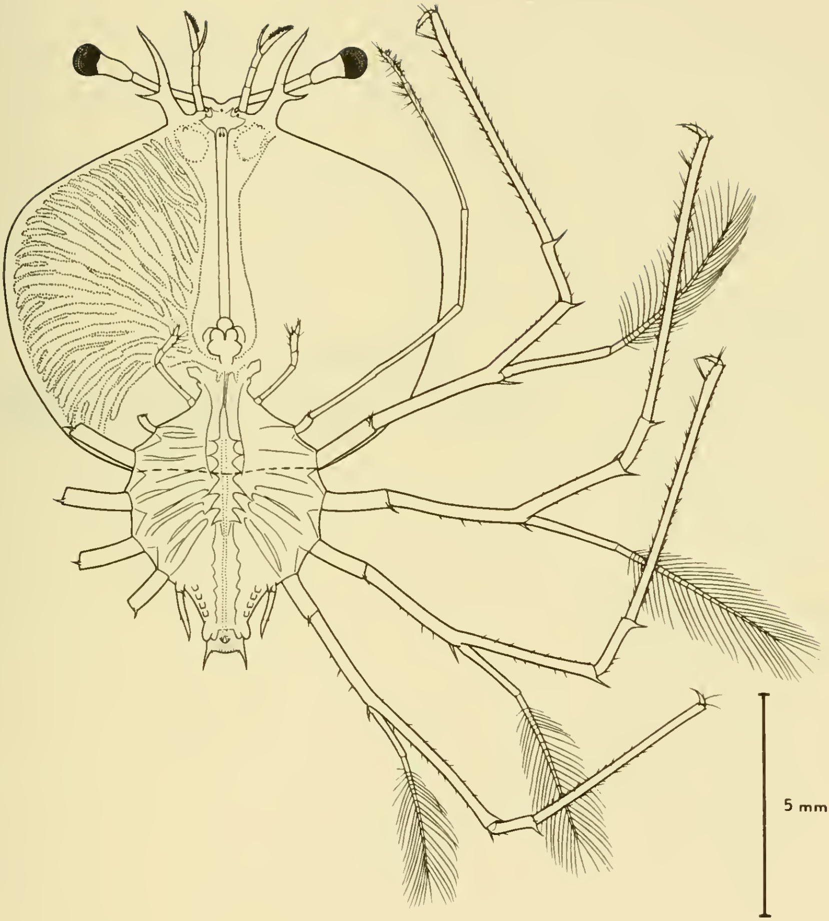

5 mm

Figure 32

Scyllarus nearctus. Stage IX, plankton.

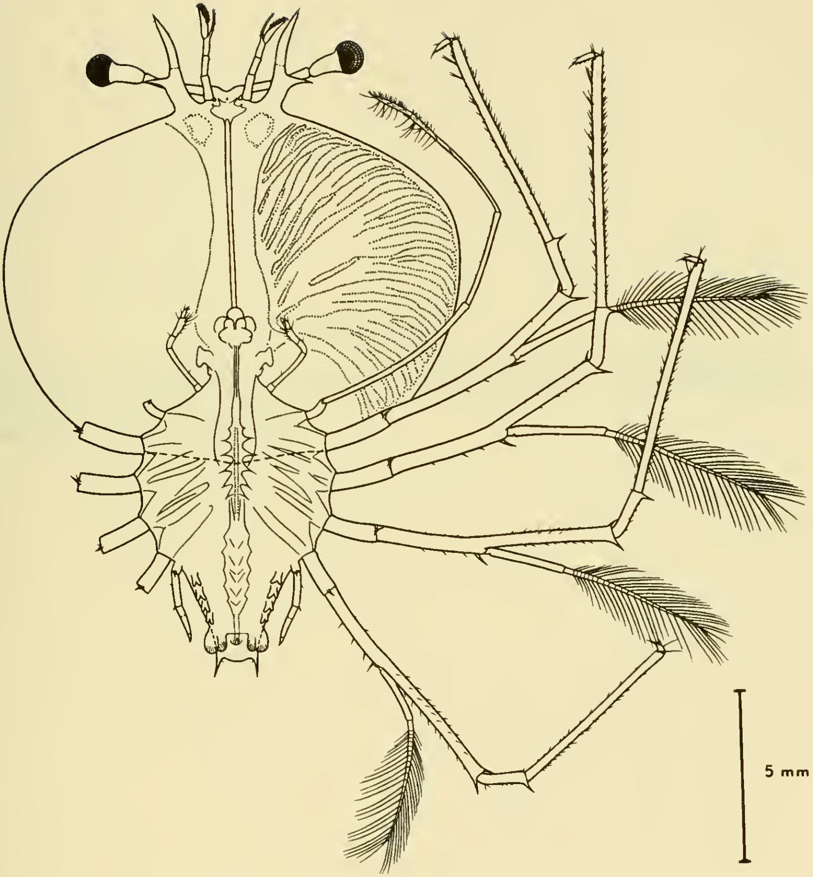

5 mm

Figure 33

Scyllarus nearctus. Stage X, from stomach of Alepisaurus, central Gulf of Mexico.

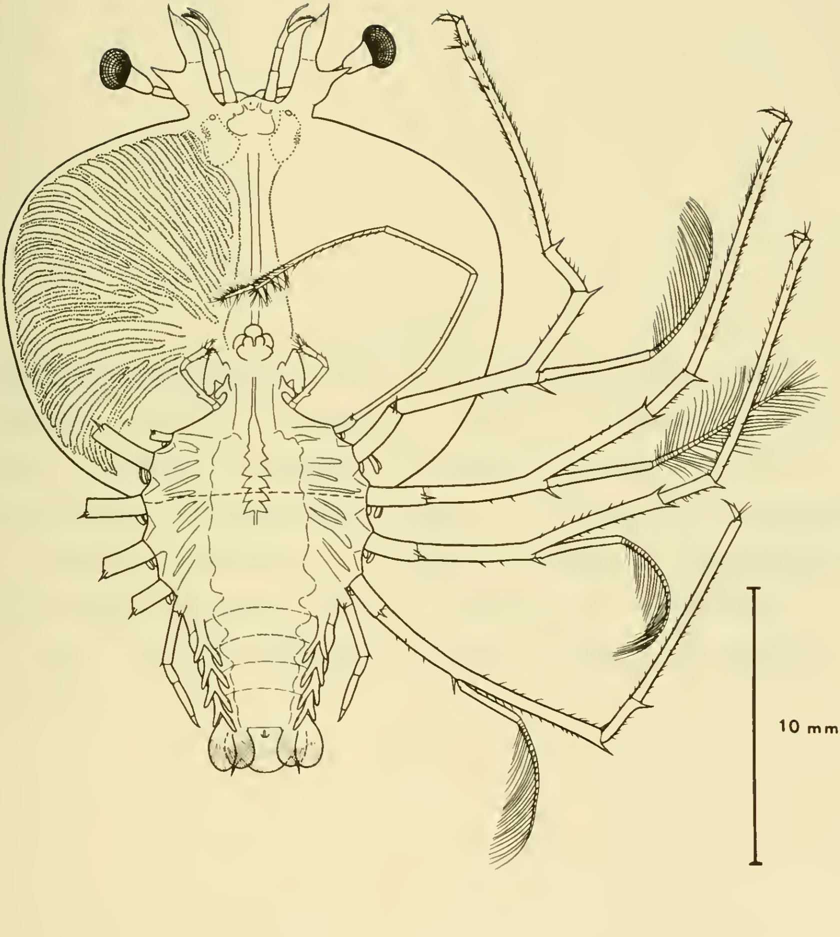

10 mm

Figure 34

Scyllarus nearctus. Abdomen of phyllosoma stages. A, stage I, reared. B, stage II, reared. C, stage III, reared. D, stage IV, reared. E, stage V, reared. F, stage VI, reared. G, stage VII, reared. H, stage VIII, plankton. I, stage IX, plankton. J, stage X, stomach of Alepisaurus. Scale ABC represents 0.2 mm; scales DE, F, G represent 0.5 mm; scale H represents 1.0 mm; scales I, J represent 3.0 mm.

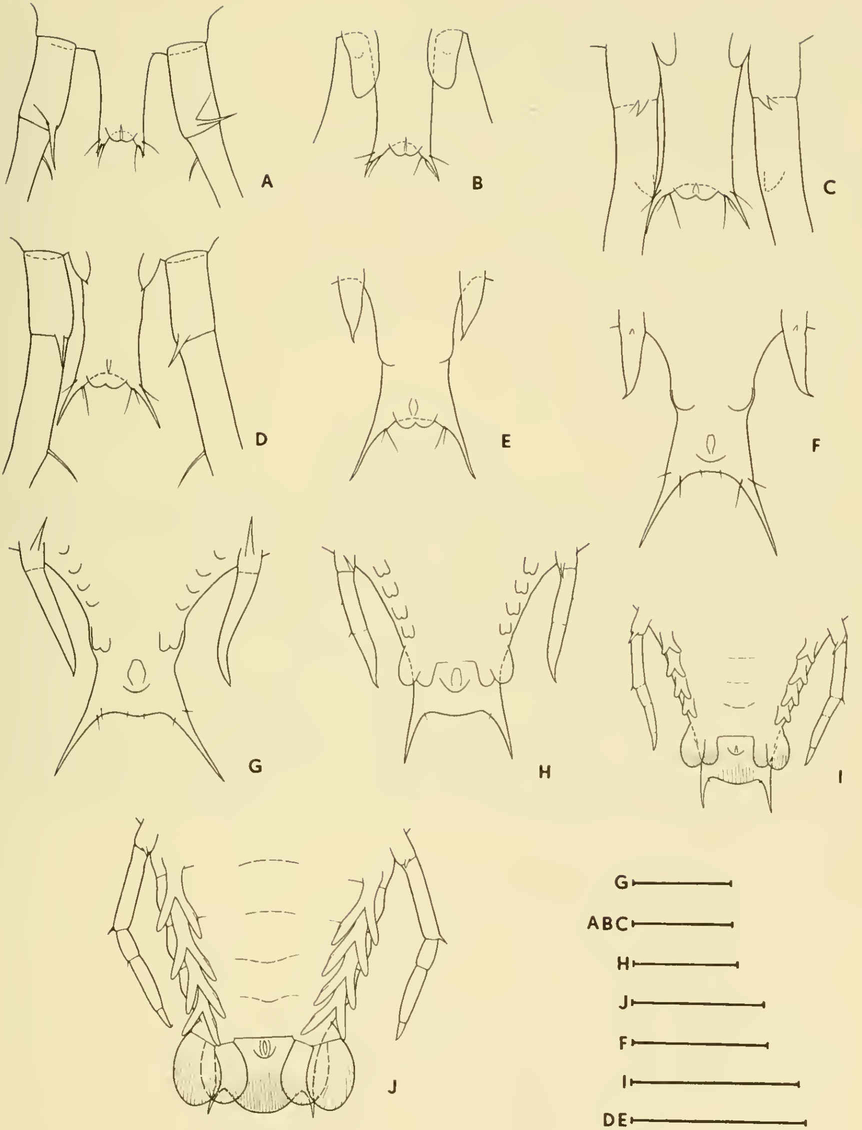

A
B
C
D
E
F
G
H
I
J
G
ABC
H
J
F
I
DE

Figure 35

Scyllarus nearctus. Antennule and antenna of phyllosoma stages. A, stage I, reared. B, stage II, reared. C, stage III, reared. D, stage IV, reared. E, stage V, reared. F, stage VI, reared. G, stage VII, reared. H, stage VIII, plankton. I, stage IX, plankton. J, stage X, stomach of Alepisaurus. Scale ABC represents 0.2 mm; scales DE, F, G represent 0.5 mm; scales H, IJ represent 1.0 mm.

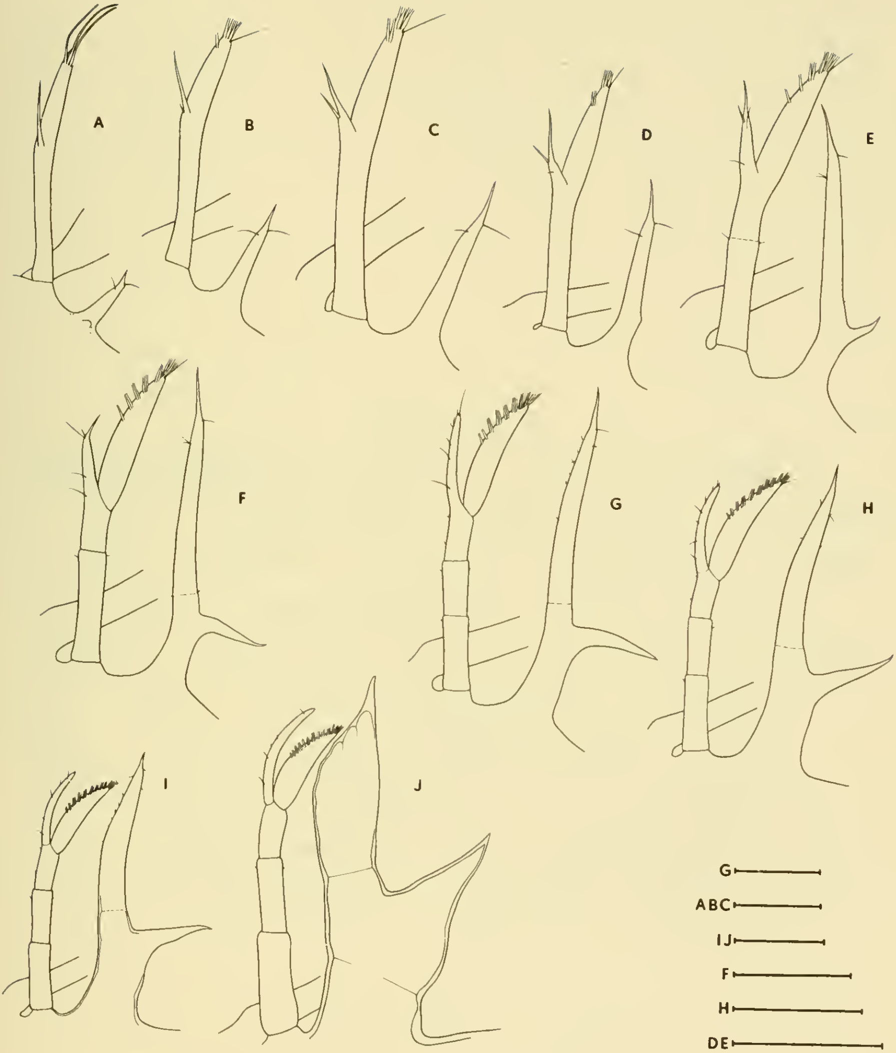

A
B
C
D
E
F
G
H
I
J
G
ABC
IJ
F
H
DE

Figure 36

Scyllarus nearctus. Mouthparts of phyllosoma stages. A, maxilla 2 and maxilliped 2, stage I, reared. B, maxilla 2, stage VI, reared. C, maxilla 2 and maxilliped 1, stage VII, reared. D, same, stage VIII, plankton. E, same, stage IX, plankton. F, maxilla 2, maxilliped 1 and maxilliped 2, stage X, stomach of Alepisaurus. G, maxilla 1, stage I, reared. H, same, stage V, reared. I, same, stage X, stomach of Alepisaurus. Scale A represents 0.2 mm; scale BCD represents 0.3 mm; scale EF represents 1.0 mm; scale GH represents 0.1 mm; scale I represents 0.5 mm.

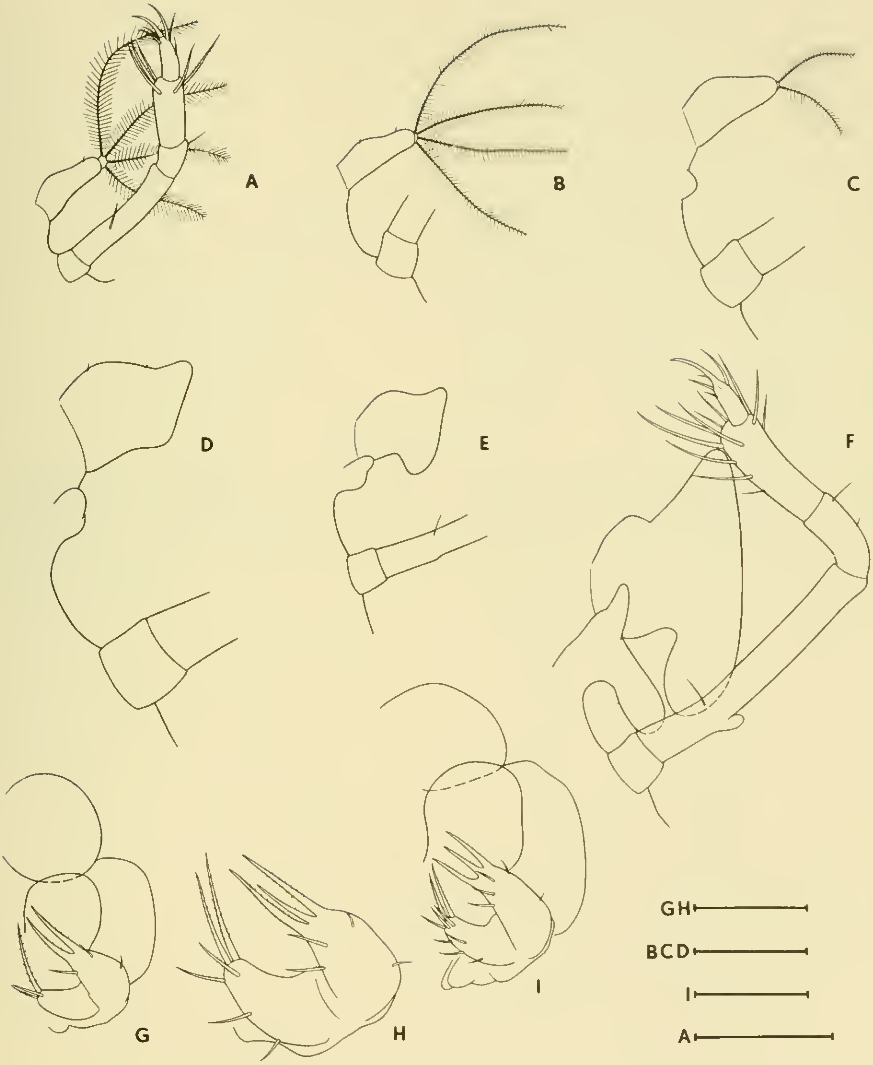

A
B
C
D
E
F
G
H
I
GH
BCD
I
A
EF

Figure 37

Scyllarus nearctus. Postlarva, from metamorphosis of planktonic phyllosoma in the laboratory. Lateral and dorsal view.

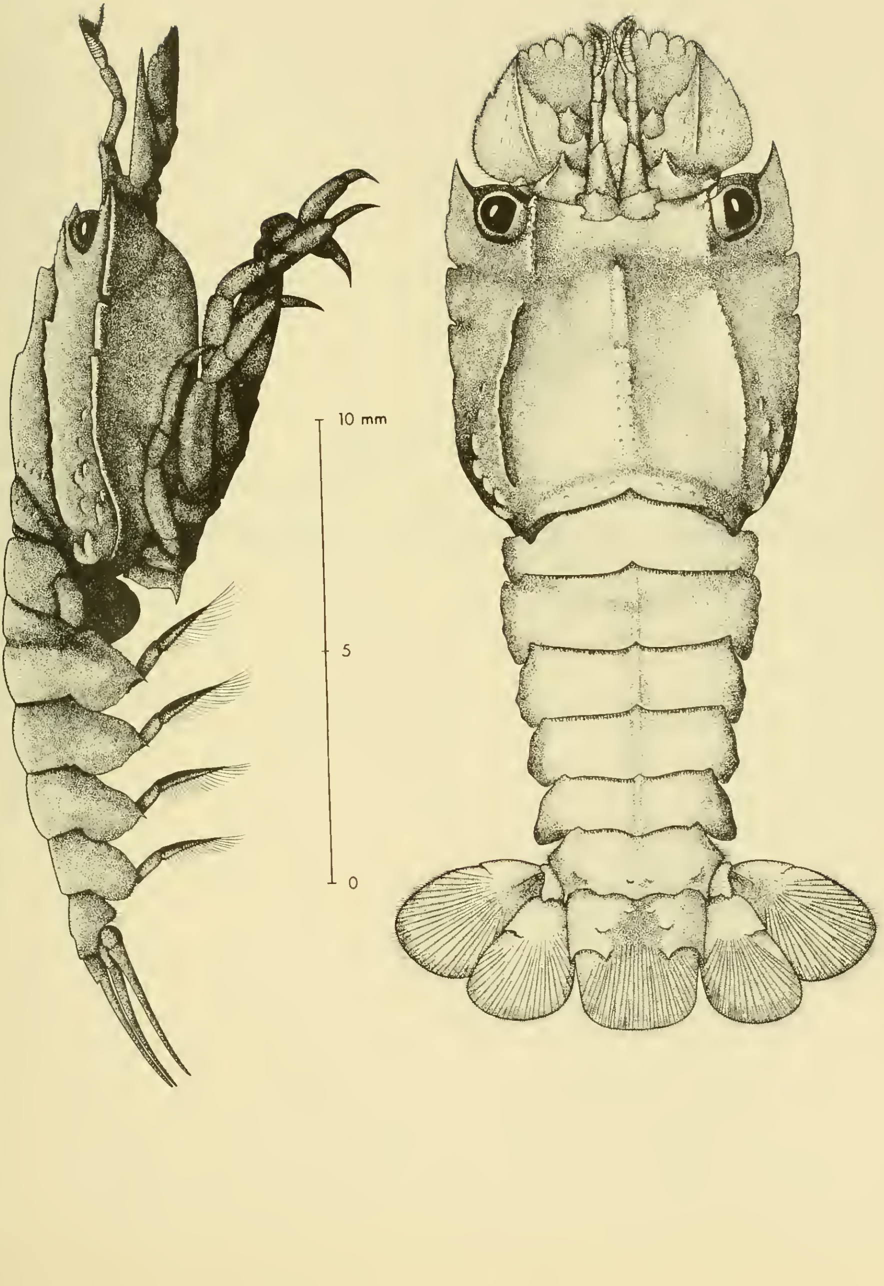

10 mm
5
0

Figure 38

Survival of starved stage I larvae of Scyllarus chacei at various temperatures. o indicates 50 per cent mortality.

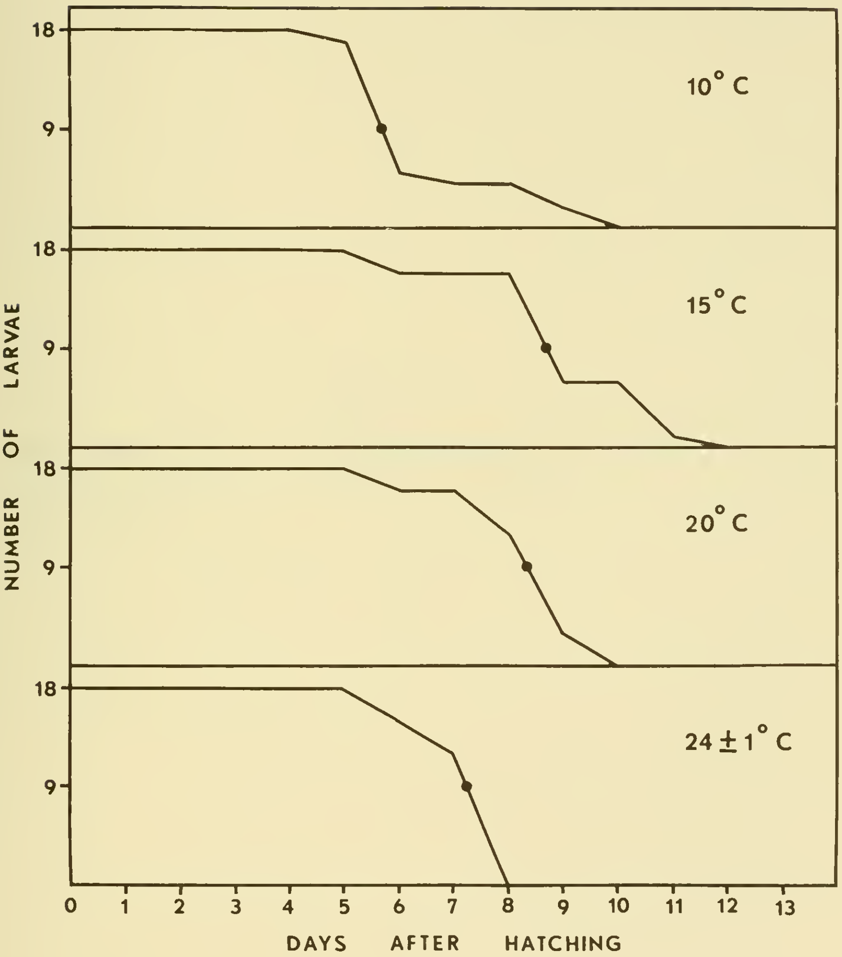

18
9
10° C
15° C
20° C
24 ± 1° C
NUMBER OF LARVAE
0
1
2
3
4
5
6
7
8
9
10
11
12
13
DAYS AFTER HATCHING

Figure 39

Larval development of _Scyllarus_ _chacei_ at various temperatures.

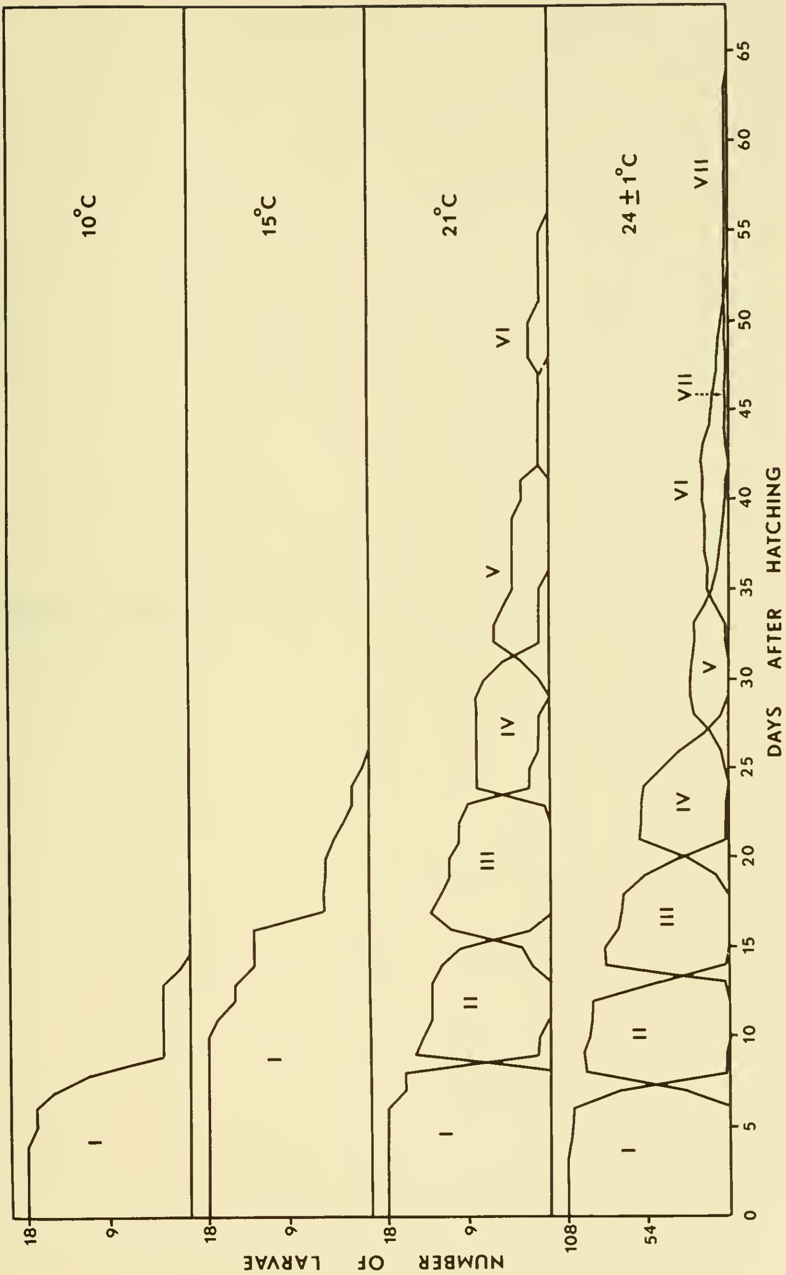

10°C
15°C
21°C
24 ± 1°C
I
II
III
IV
V
VI
VII
18
9
108
54
NUMBER OF LARVAE
DAYS AFTER HATCHING
0
5
10
15
20
25
30
35
40
45
50
55
60
65

Figure 40

Scyllarus *chacei*. Stage I, reared. Scale represents 1.0 mm.

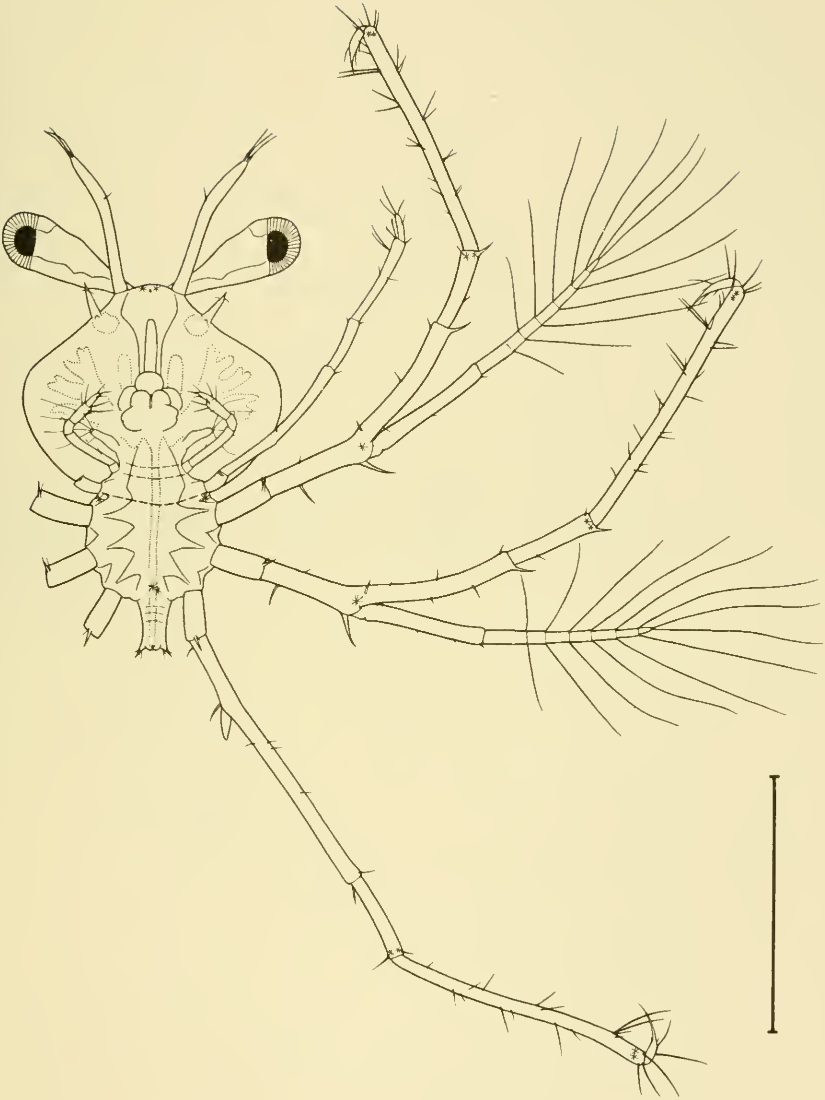


Figure 41

Scyllarus chacei. Stage II, reared. Scale represents 1.0 mm.

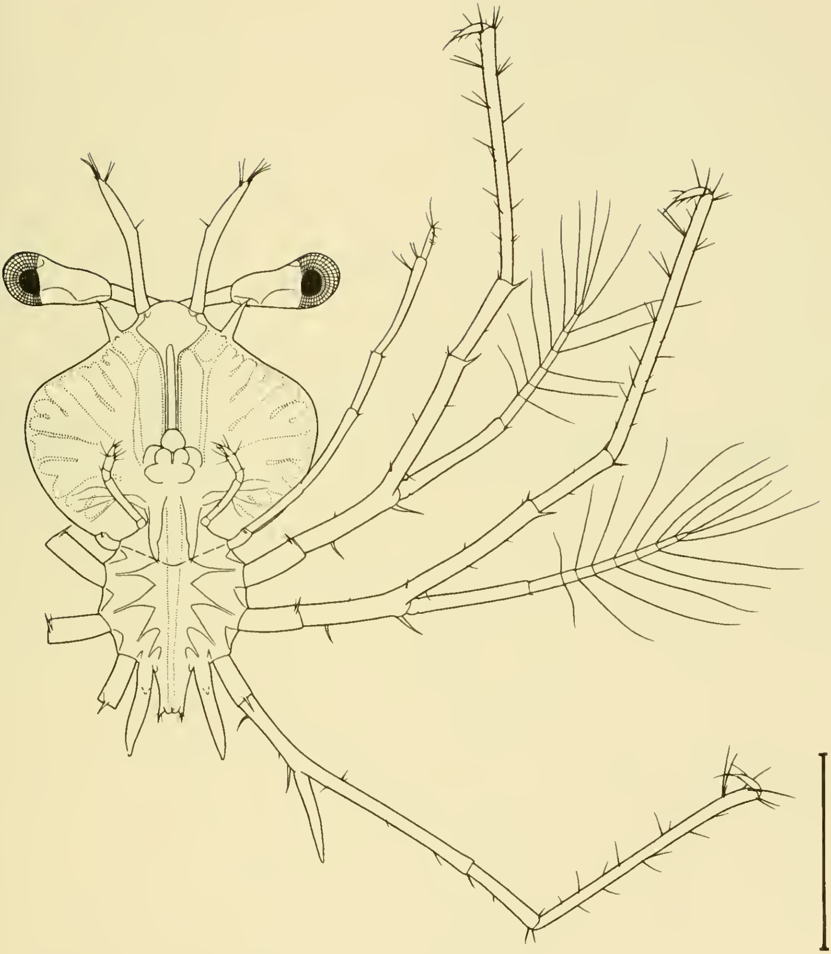


Figure 42

Scyllarus chacei. Stage III, reared. Scale represents 1.0 mm.

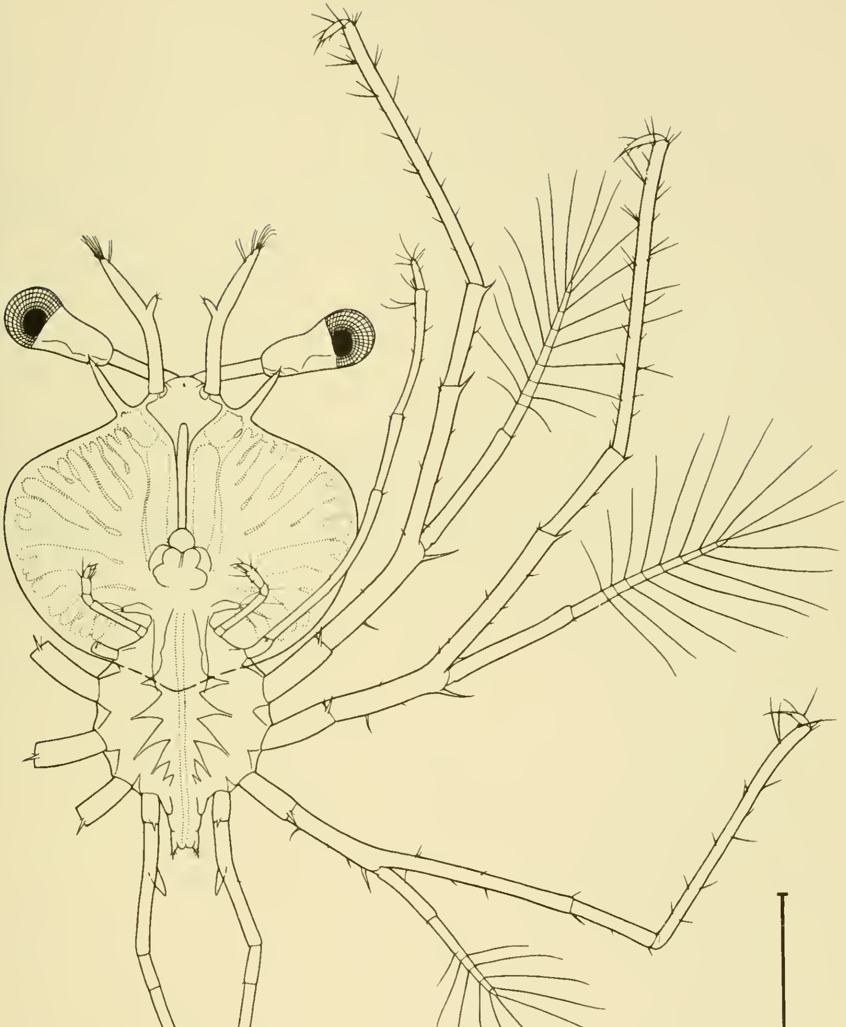


Figure 43

Scyllarus chacei. Stage IV, reared. Scale represents 1.0 mm.

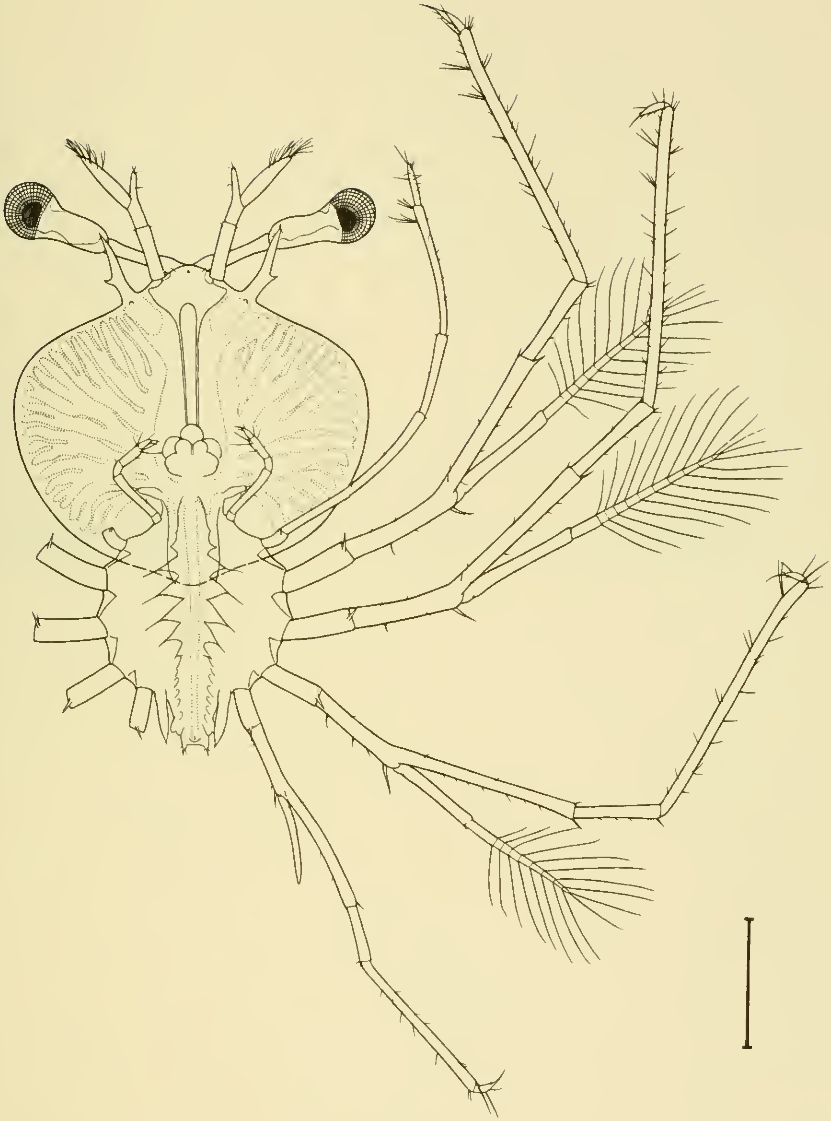


Figure 44

Scyllarus chacei. Stage V, reared. Scale represents 1.0 mm.

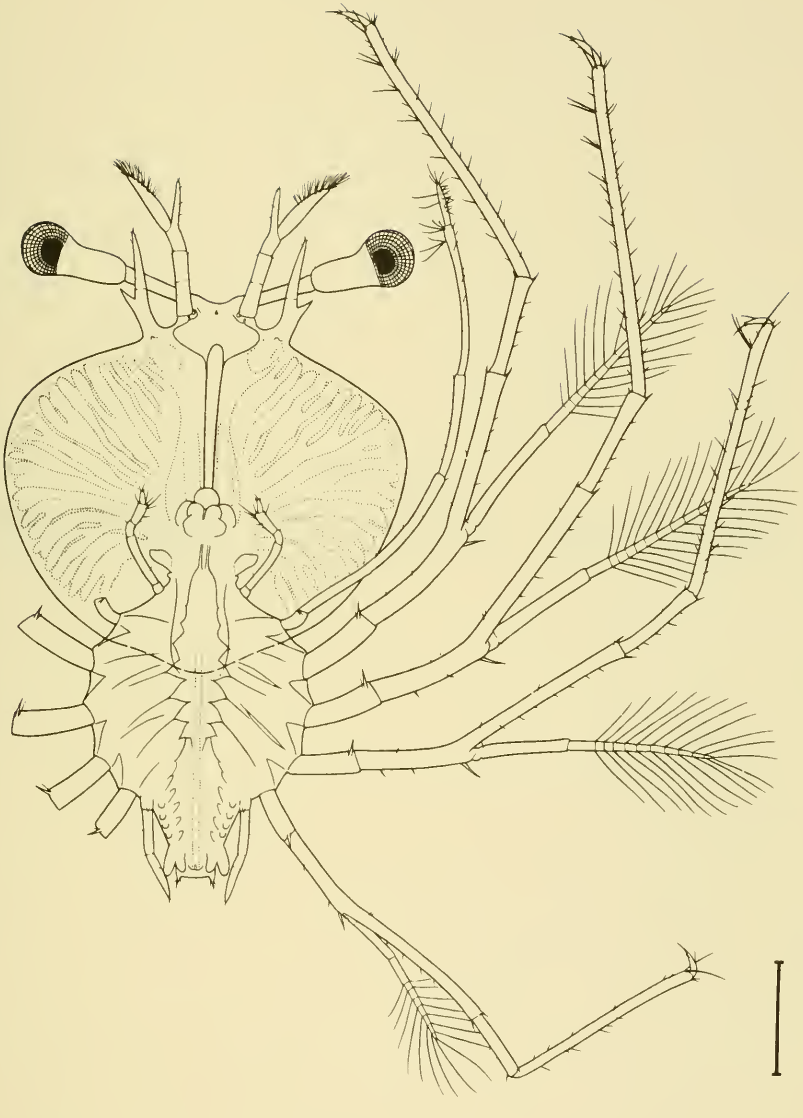


Figure 45

Scyllarus chacei. Stage VI, reared. Scale represents 1.0 mm.

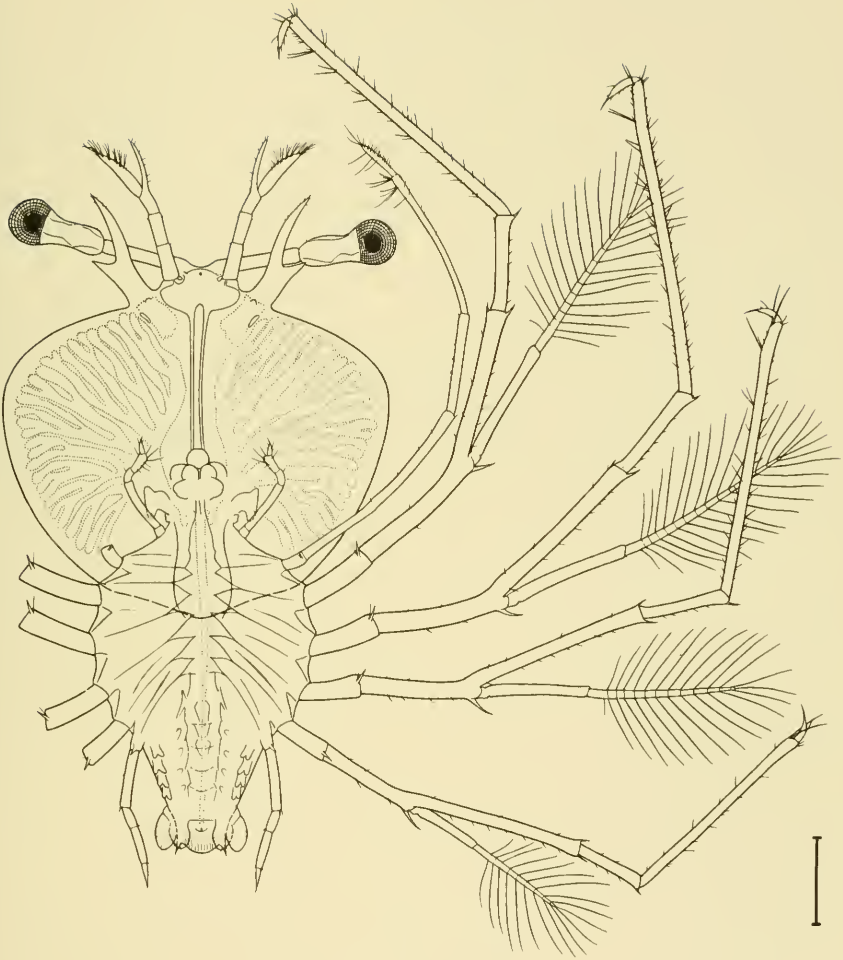


Figure 46

Scyllarus *chacei*. Stage VII, reared.

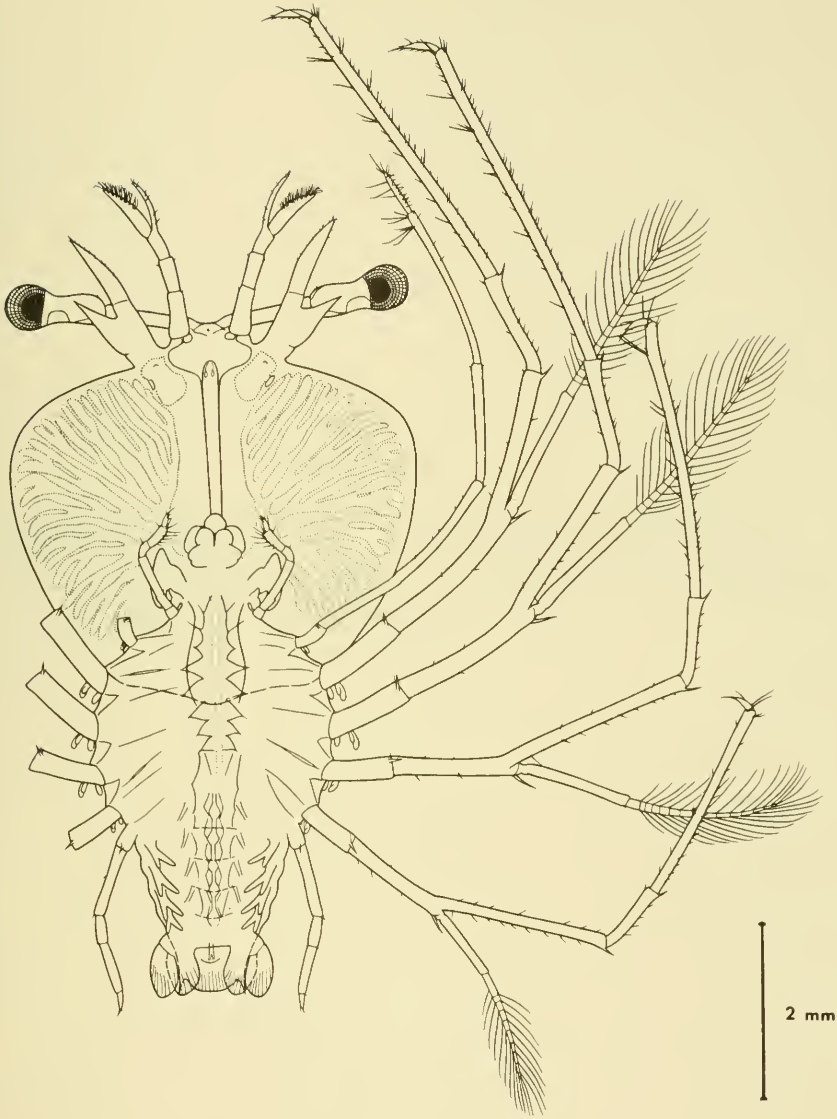
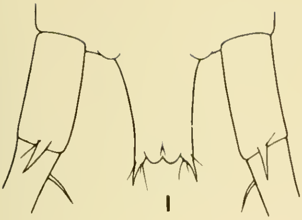
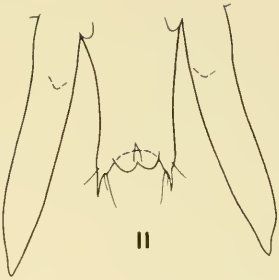

2 mm

Figure 47

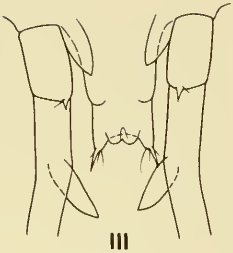
Scyllarus chacei. Abdomen of phyllosoma stages I-VII. Scale I II represents 0.2 mm; scales III IV, V represent 0.5 mm; scale VI VII represents 1.0 mm.



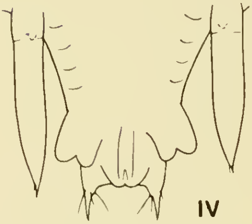
I



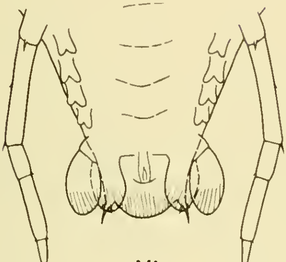
II



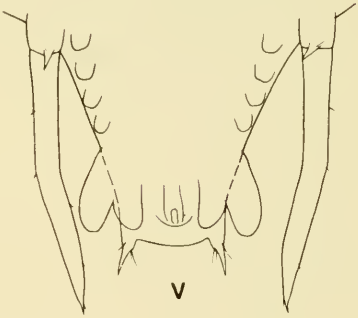
III



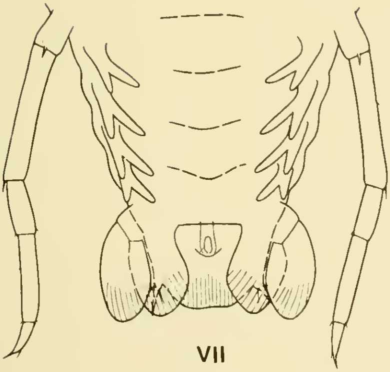
IV



VI



V



VII

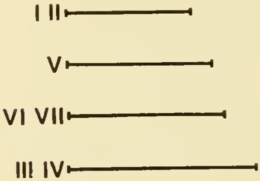


Figure 48

Scyllarus chacei. Antennule and antenna of phyllosoma stages I-VII. Scale I II represents 0.3 mm; scales III IV, V represent 0.5 mm; scale VI VII represents 1.0 mm.

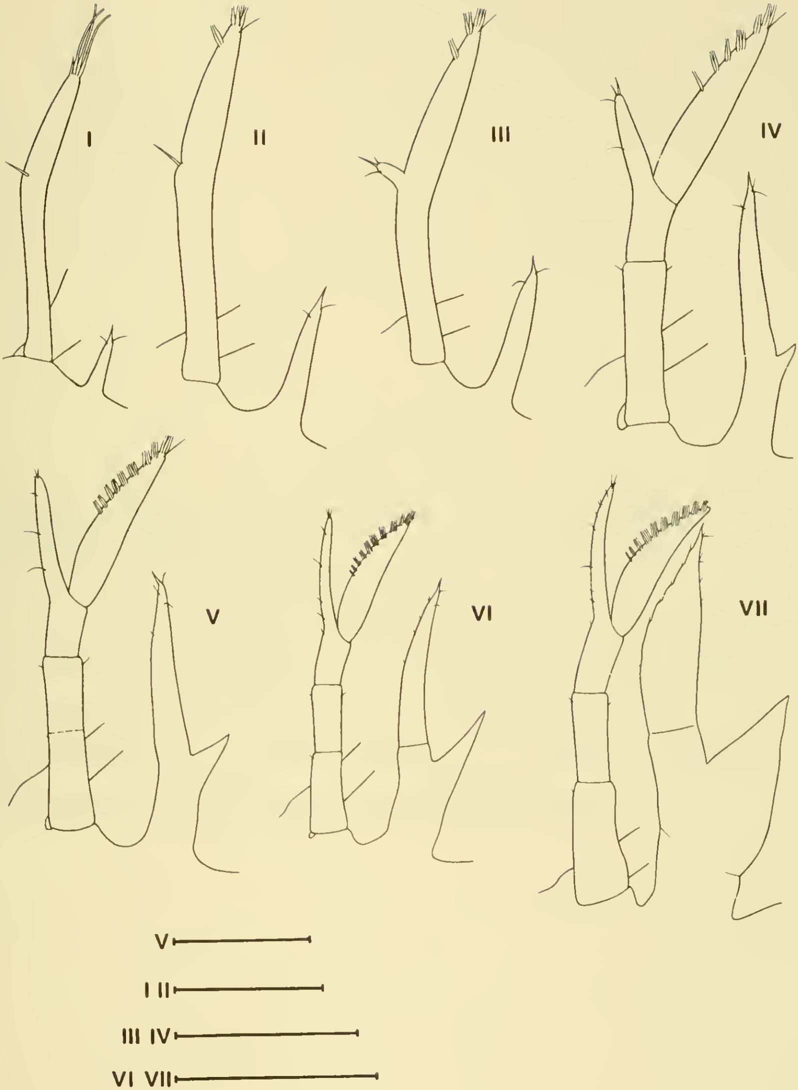

I
II
III
IV
V
VI
VII
V
I II
III IV
VI VII

Figure 49

Scyllarus chacei. Mouthparts of phyllosoma stages. A, maxilla 2 and maxilliped 2, stage I. B, maxilla 2, stage IV. C, maxilla 2 and maxilliped 1, stage V. D, maxilla 2 and maxilliped 1, stage VI. E, maxilla 2, maxilliped 1 and maxilliped 2, stage VII. F, maxilla 1, stage I. G, same, stage IV. H, same, stage VII. Scales ABC, FG and H represent 0.2 mm; scale DE represents 0.5 mm.

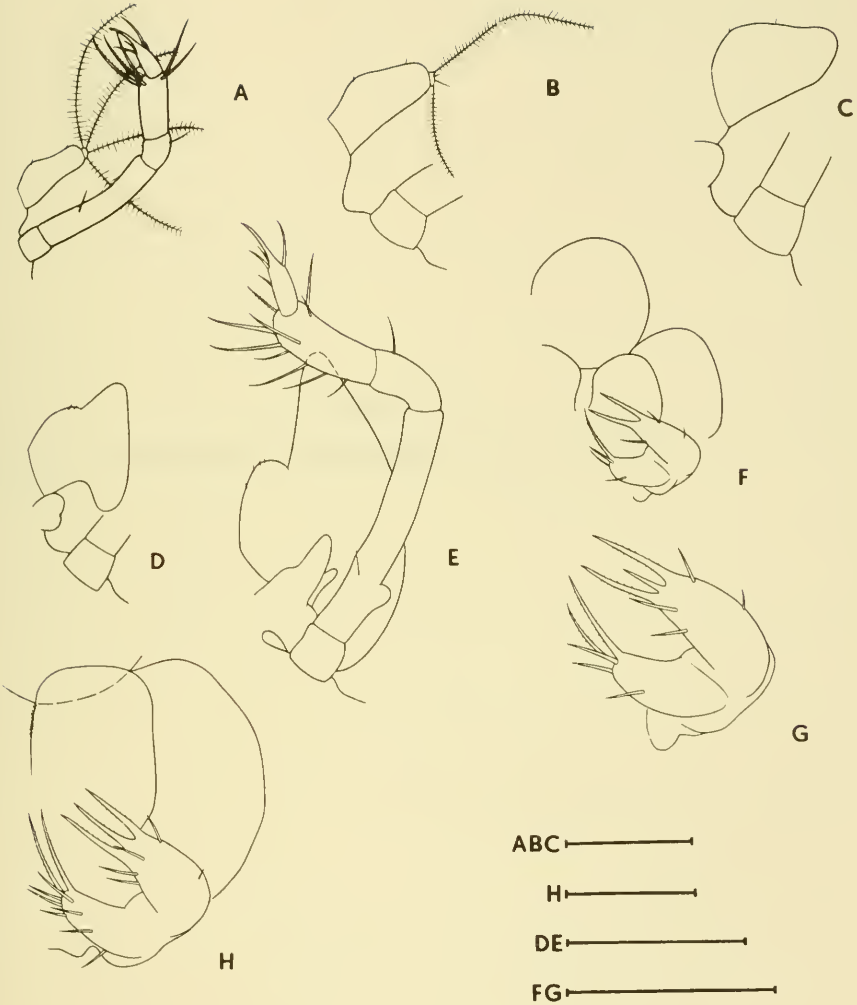

A
B
C
D
E
F
G
H
ABC
H
DE
FG

Figure 50

Larval development of _Scyllarus_ n. sp. at 25°C.

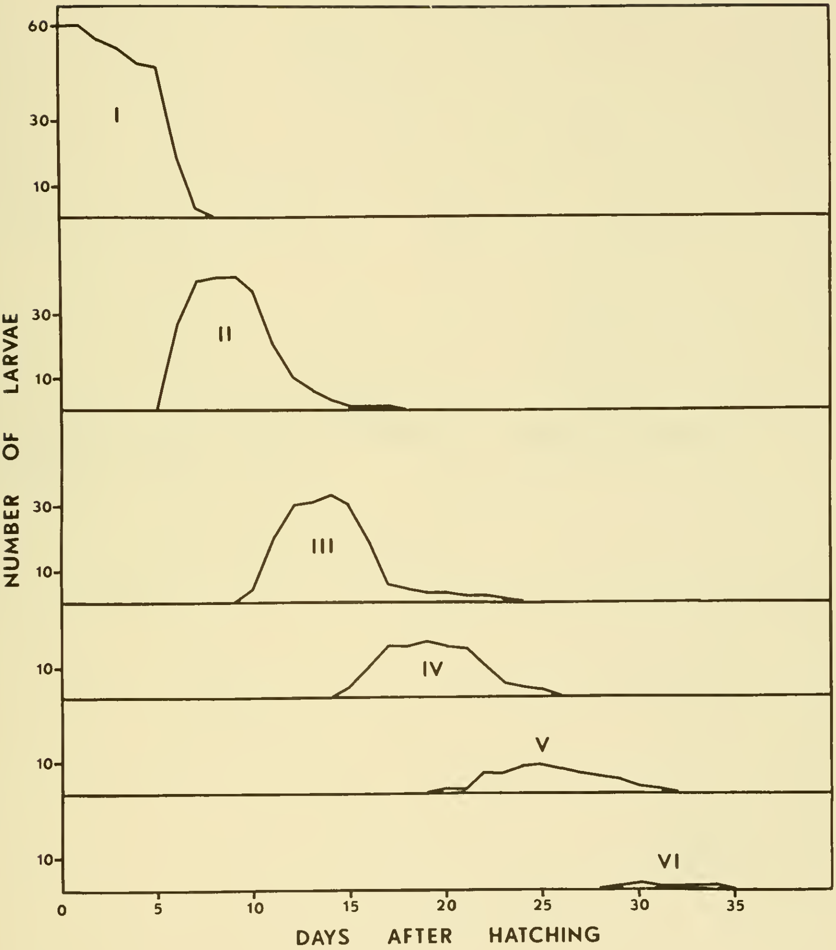

60
30
10
I
30
10
II
30
10
III
10
IV
10
V
10
VI
NUMBER OF LARVAE
0
5
10
15
20
25
30
35
DAYS AFTER HATCHING

Figure 51

Scyllarus n. sp. Stage I, reared. Scale represents 1.0 mm.

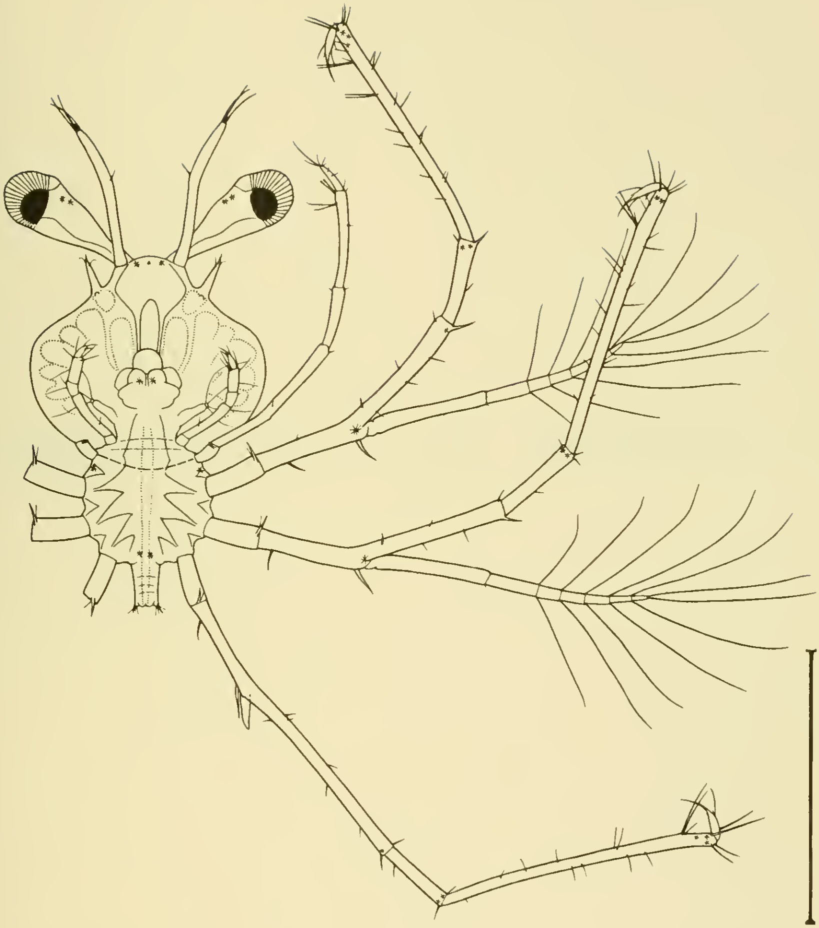


Figure 52

Scyllarus n. sp. Stage II, reared. Scale represents 1.0 mm.

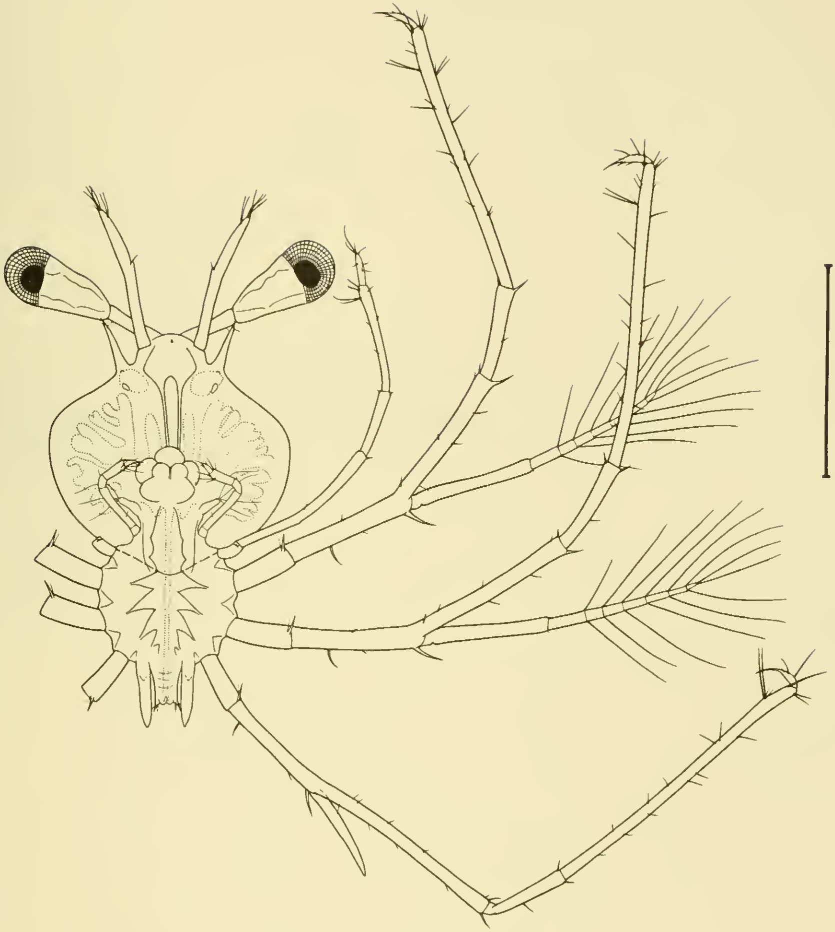


Figure 53

Scyllarus n. sp. Stage III, reared. Scale represents 1.0 mm.

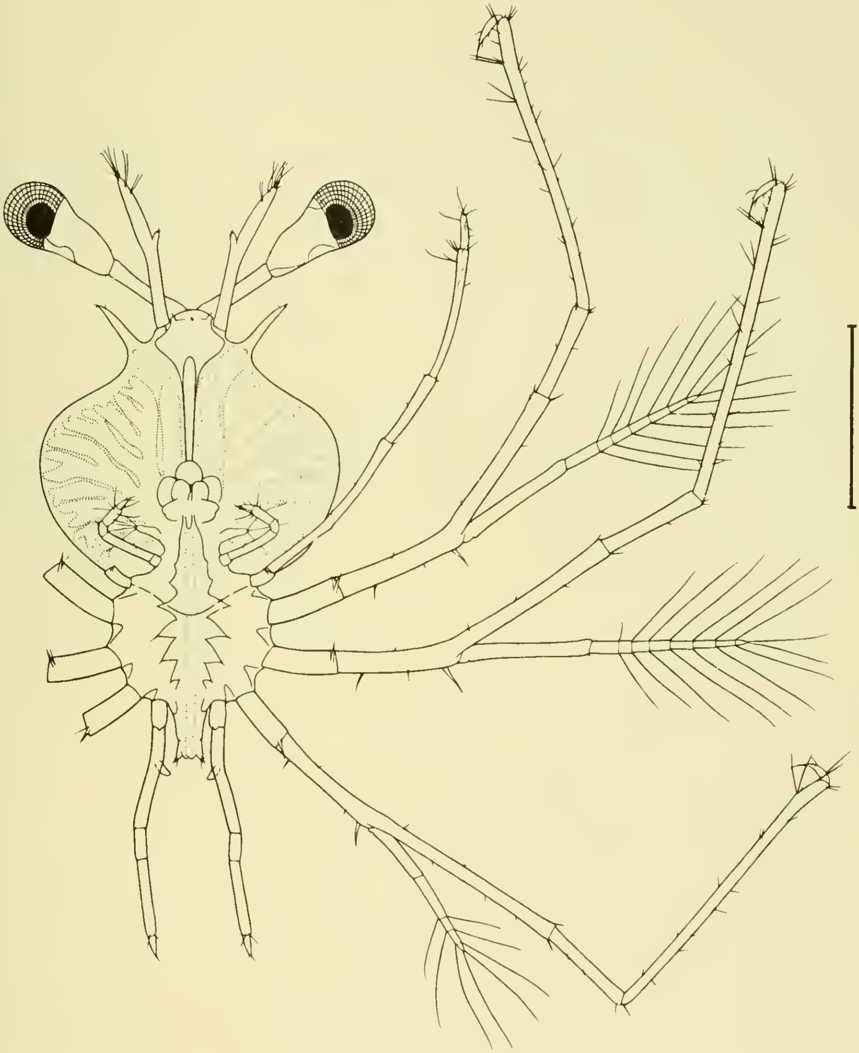


Figure 54

Scyllarus n. sp. Stage IV, reared. Scale represents 1.0 mm.

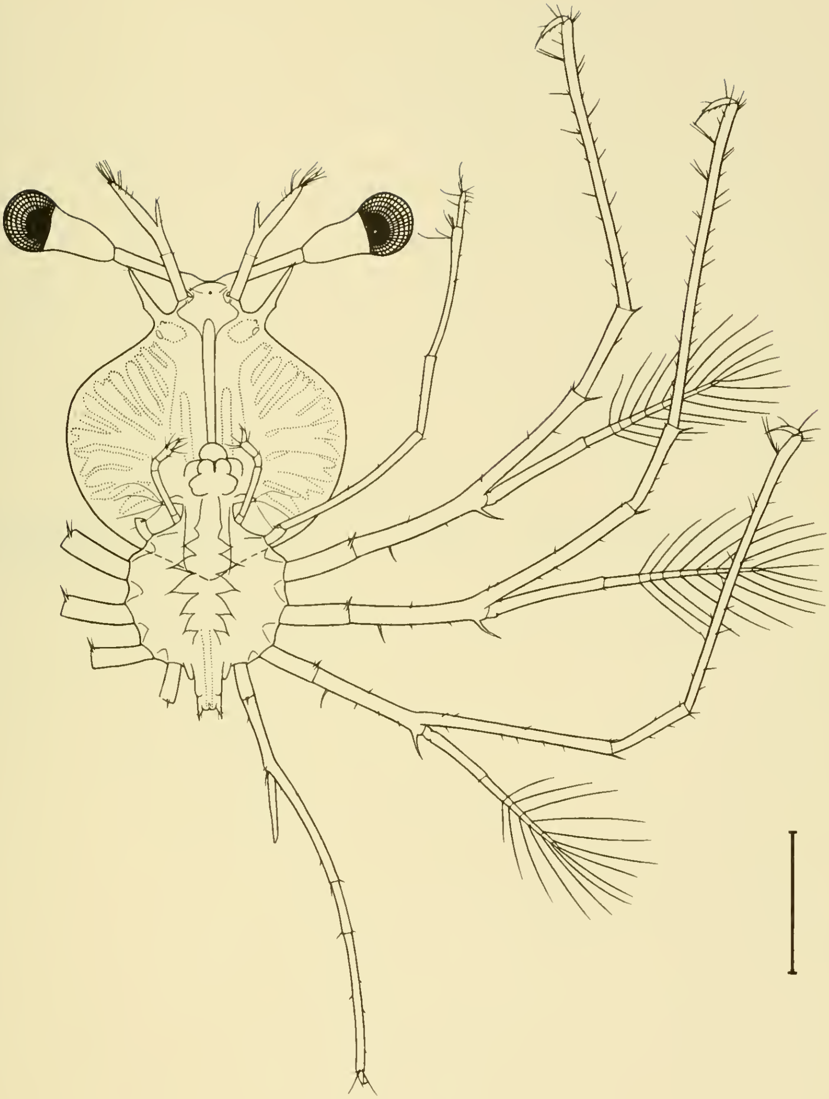


Figure 55

Scyllarus n. sp. Stage V, reared. Scale represents 1.0 mm.

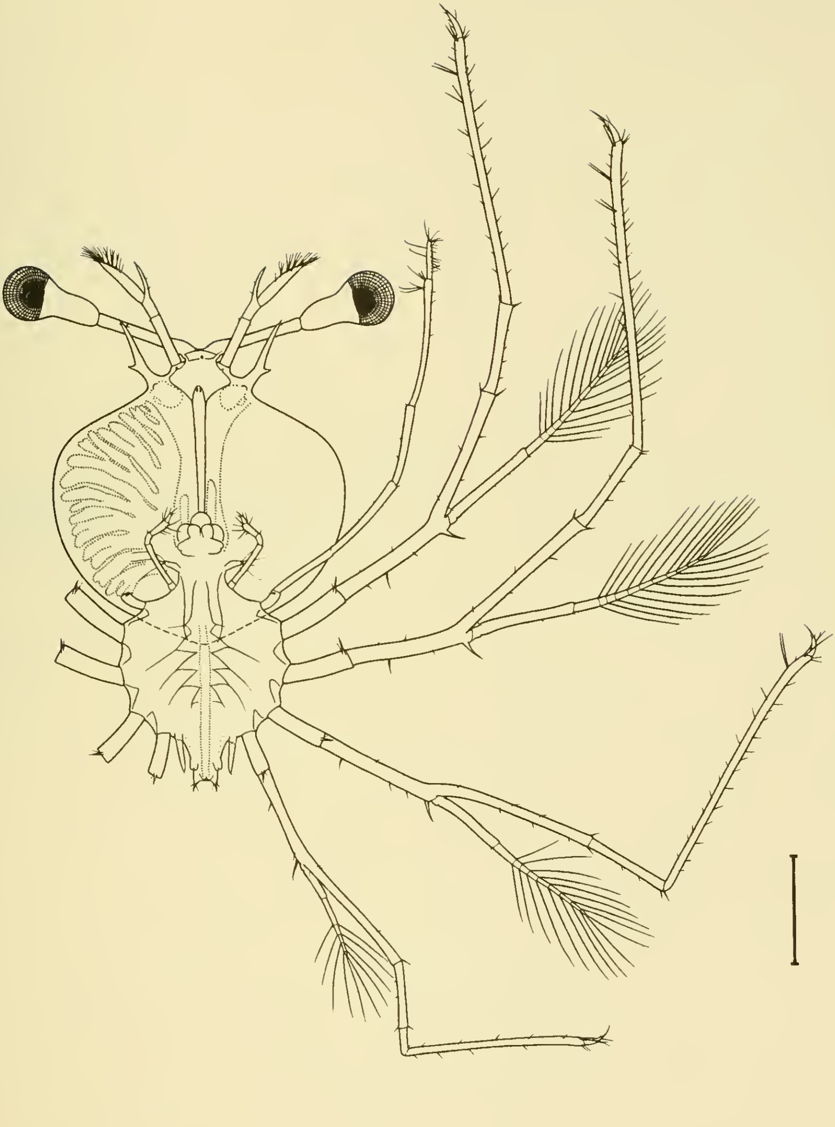


Figure 56

Scyllarus n. sp. Stage VI, reared. Scale represents 1.0 mm.

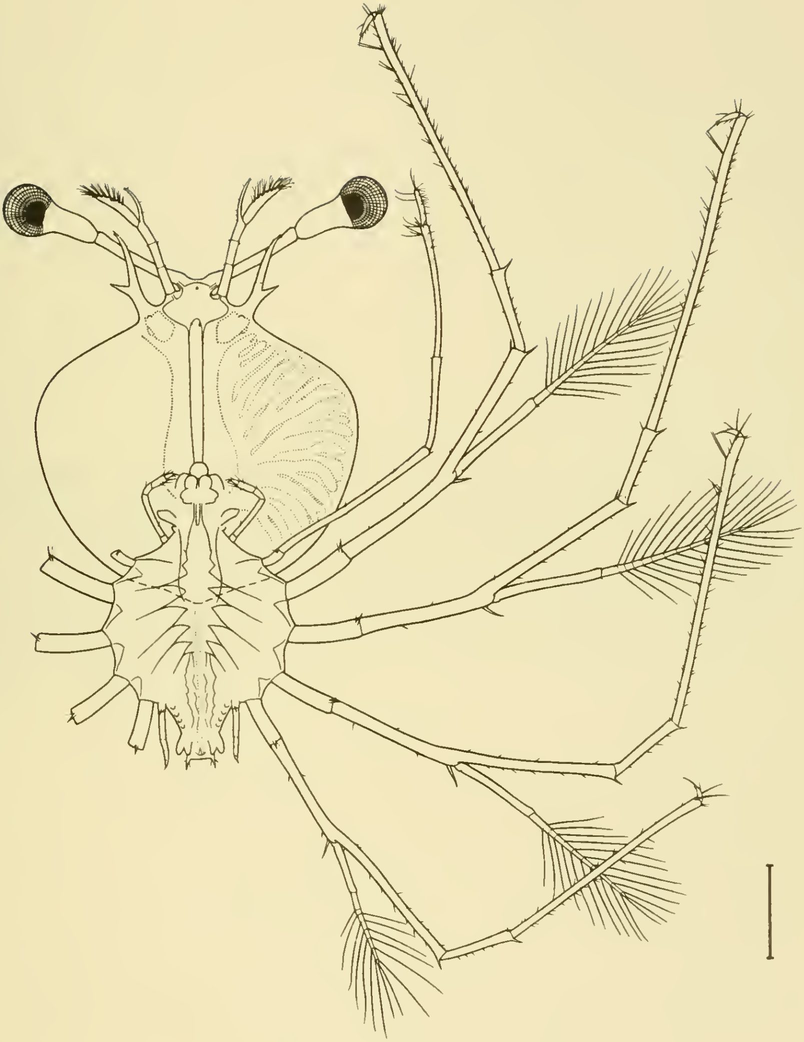


Figure 57

Scyllarus n. sp. Abdomen of phyllosoma stages. A, stage I. B, stage II. C, stage III. D, stage IV. E, stage V. F, stage VI. G, most advanced stage VI individual. Scales AB, C represent 0.2 mm; scales D, EF represent 0.5 mm; scale G represents 1.0 mm.

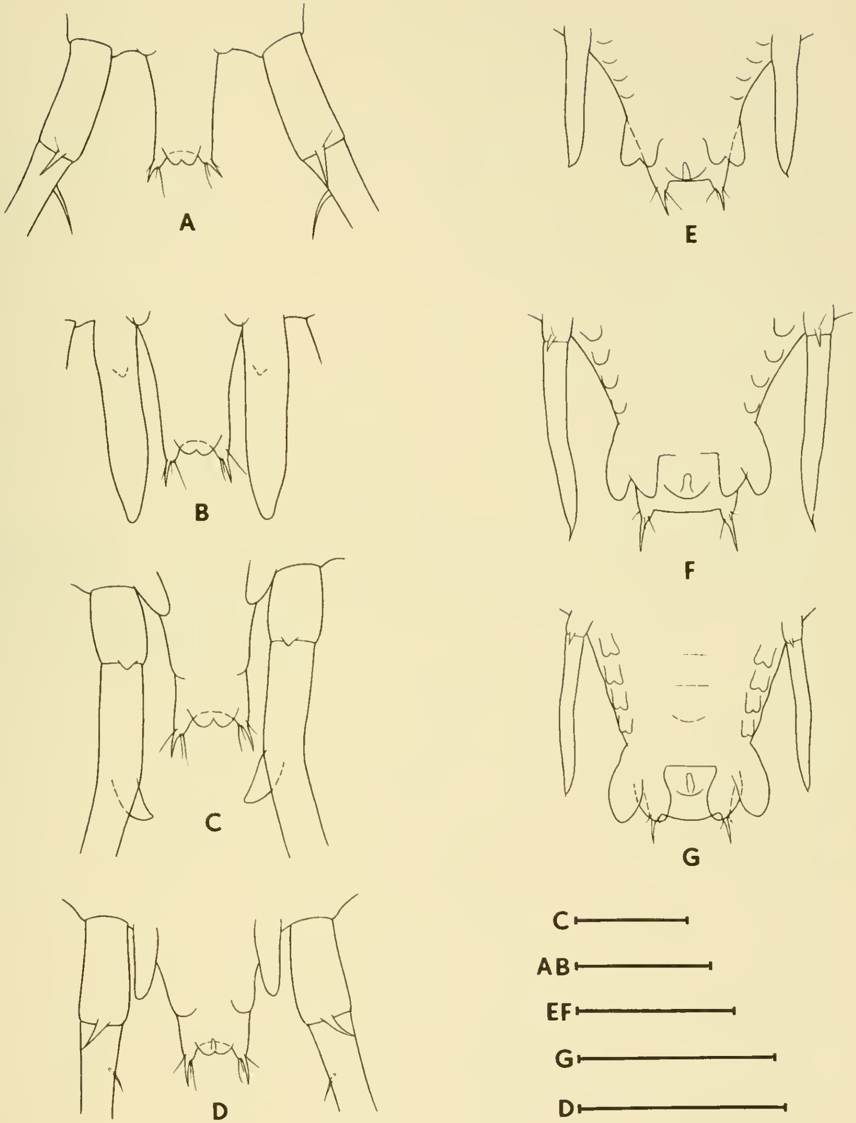

A
E
B
F
C
G
D
C
AB
EF
G
D

Figure 58

Scyllarus n. sp. Antennule and antenna of phyllosoma stages I-VI. Scale I II represents 0.3 mm; scales III IV, V VI represent 0.5 mm.

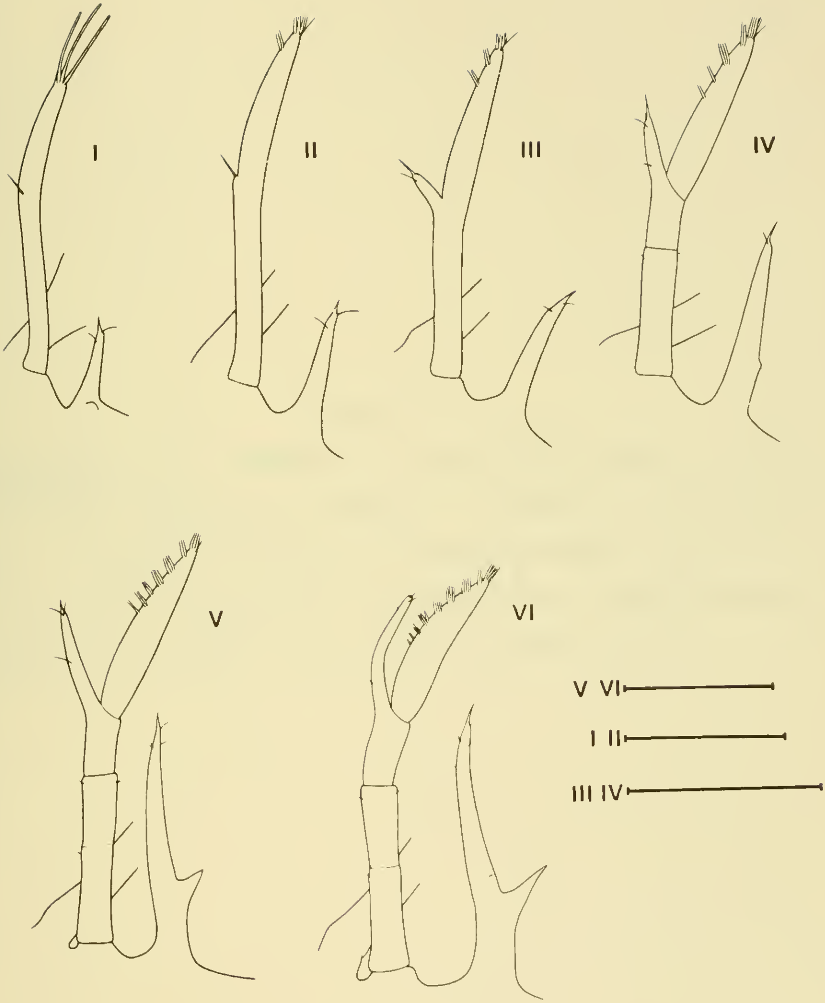

I
II
III
IV
V
VI
V VI
I II
III IV

Figure 59

Scyllarus n. sp. Mouthparts of phyllosoma stages. A, maxilla 2 and maxilliped 2, stage I. B, maxilla 2 and maxilliped 1, stage V. C, maxilla 2 and maxilliped 1, stage VI. D, maxilla 2, maxilliped 1 and maxilliped 2, most advanced stage VI individual. All scales represent 0.2 mm.

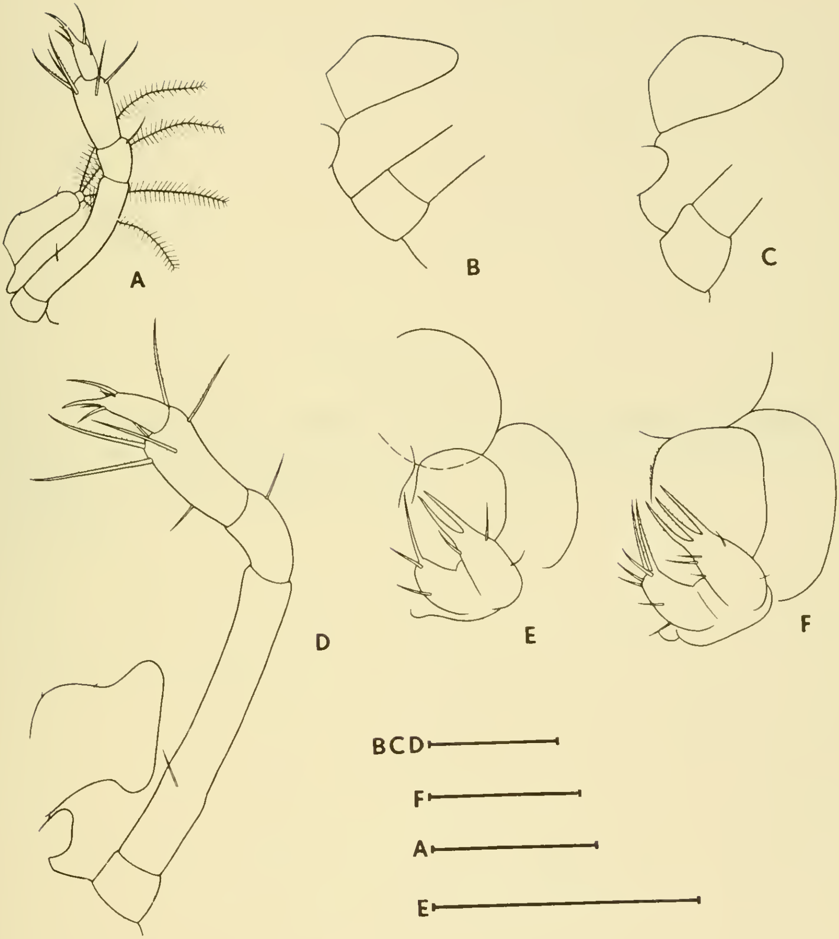

A
B
C
D
E
F
BCD
F
A
E

Figure 60

Survival of starved stage I larvae of _Scyllarides aequinoctialis_ at various temperatures. o indicates 50 per cent mortality.

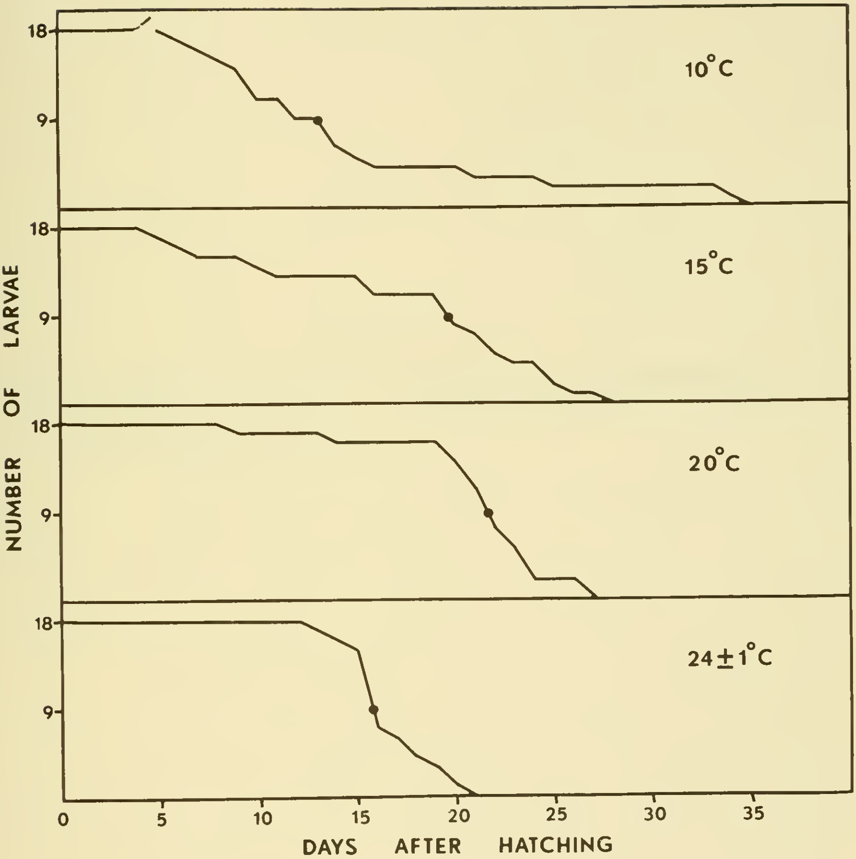

18
9
10°C
18
9
15°C
18
9
20°C
18
9
24±1°C
NUMBER OF LARVAE
0
5
10
15
20
25
30
35
DAYS AFTER HATCHING

Figure 61

Early larval development of *Scyllarides aequinoctialis* at various temperatures.

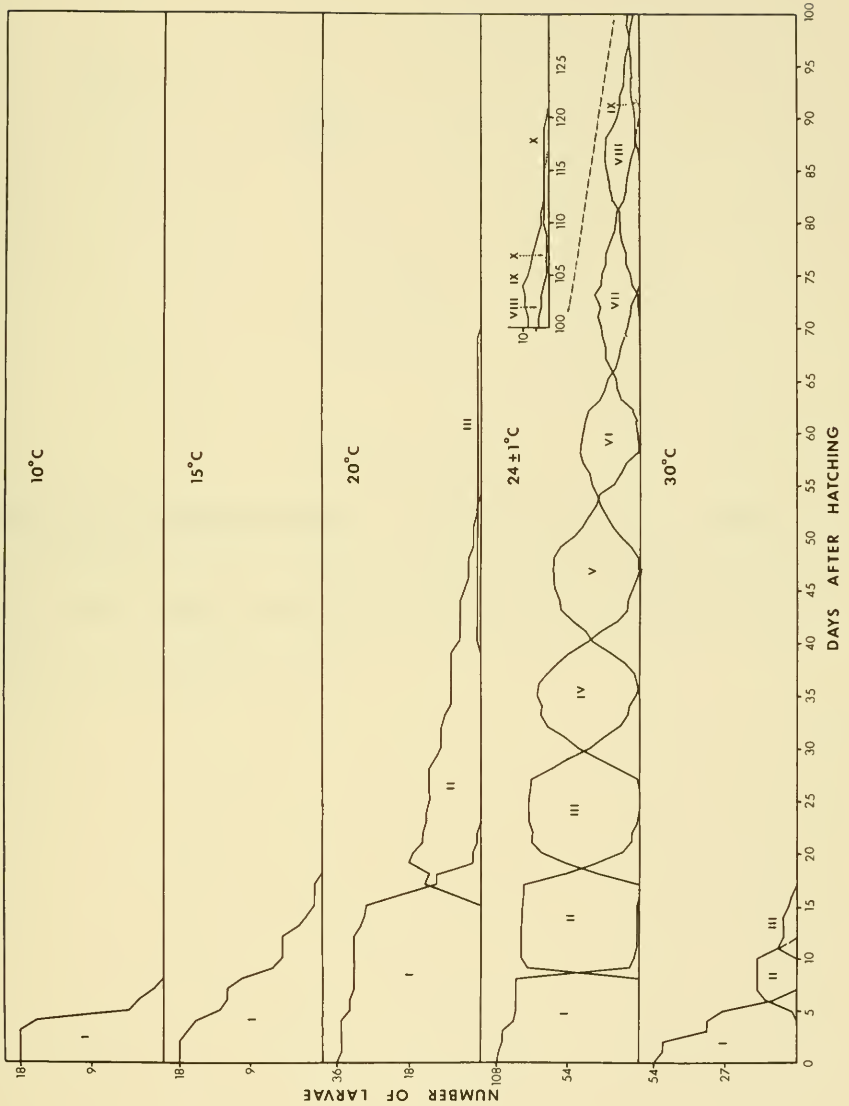

10°C
15°C
20°C
24 ± 1°C
30°C
I
II
III
IV
V
VI
VII
VIII
IX
X
18
9
18
9
36
18
108
54
54
27
10
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
85
90
95
100
100
105
110
115
120
125
NUMBER OF LARVAE
DAYS AFTER HATCHING

Figure 62

Scyllarides aequinoctialis. Naupliosoma stage, hatched in the laboratory. The legs, which are folded anteriorly over the thorax, have been extended to facilitate illustration. Scale represents 1.0 mm.

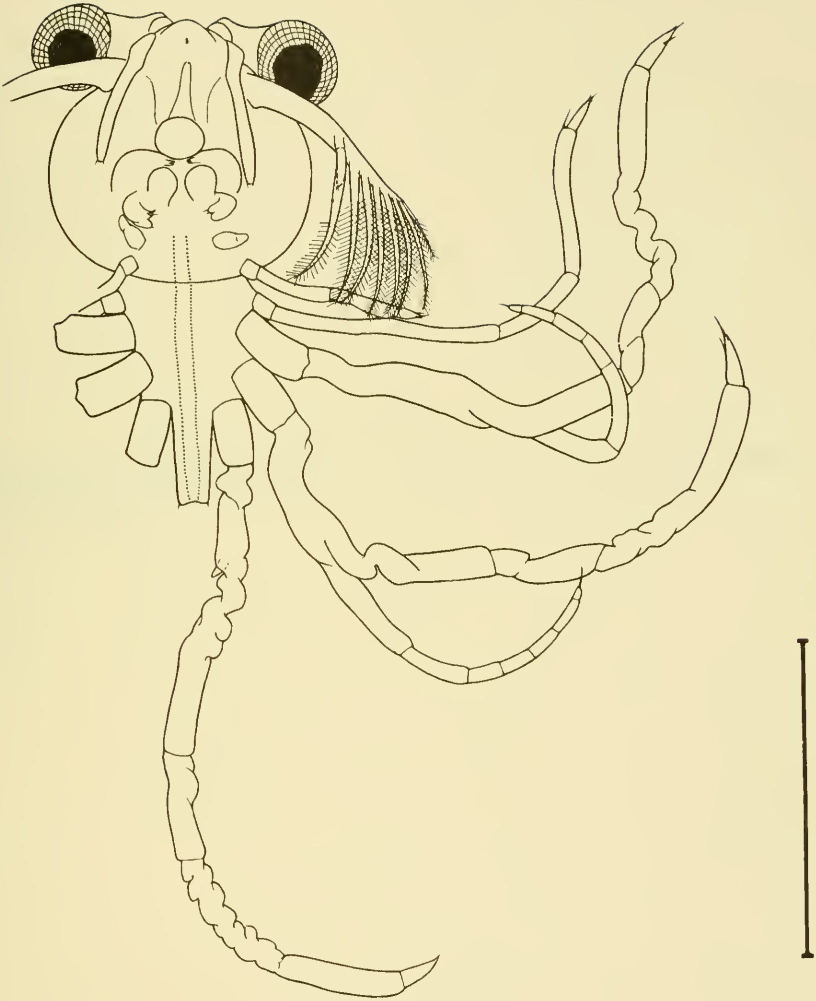


Figure 63

Scyllarides aequinoctialis. Stage I, reared. Scale represents 1.0 mm.

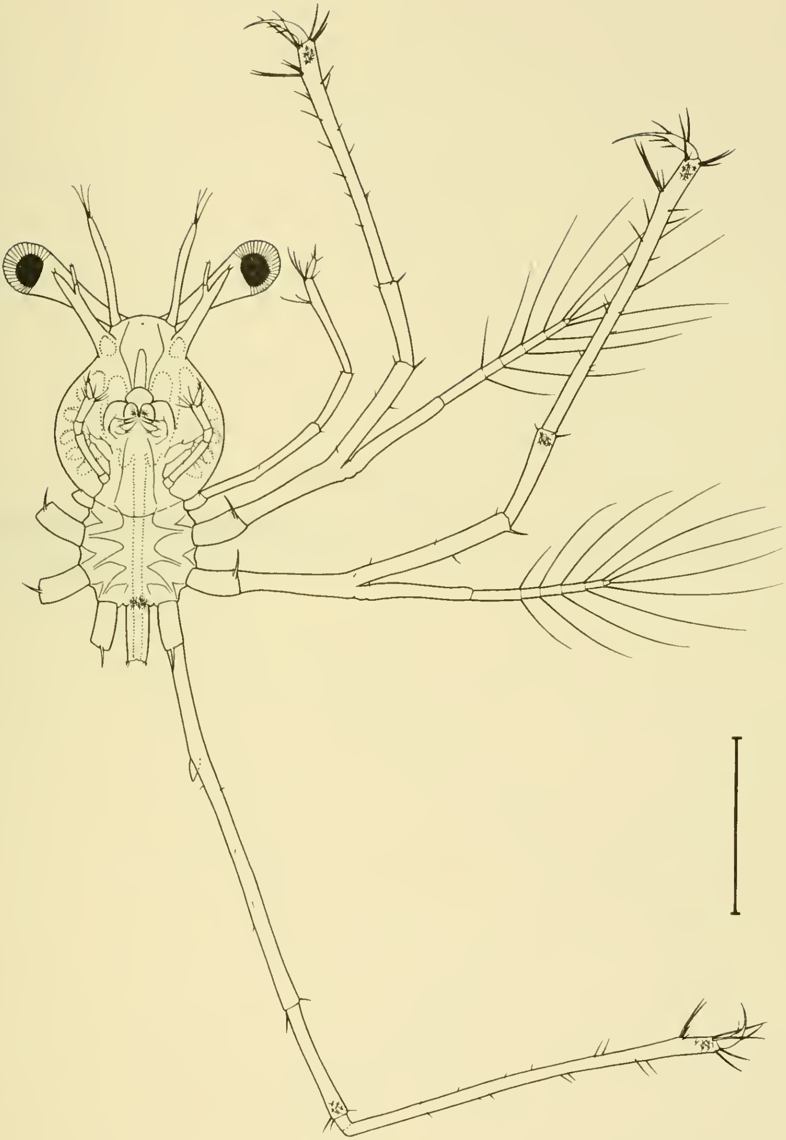


Figure 64

Scyllarides aequinoctialis. Stage II, reared. Scale represents 1.0 mm.

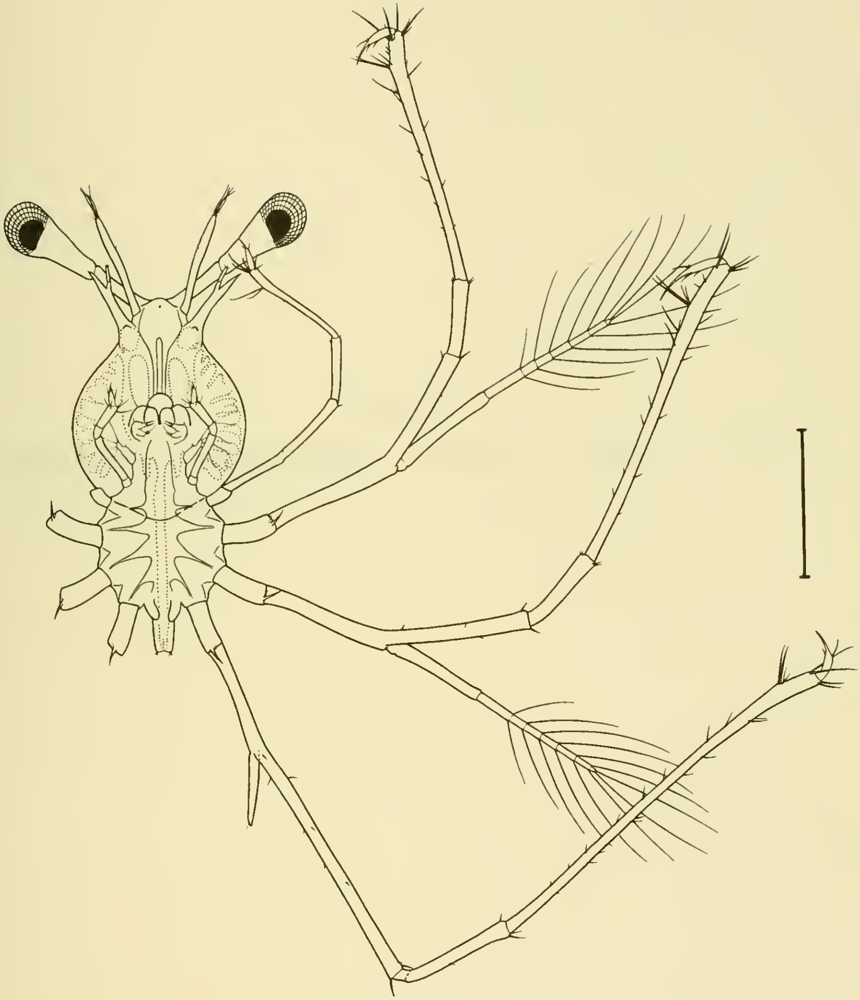


Figure 65

Scyllarides aequinoctialis. Stage III, reared. Scale represents 1.0 mm.

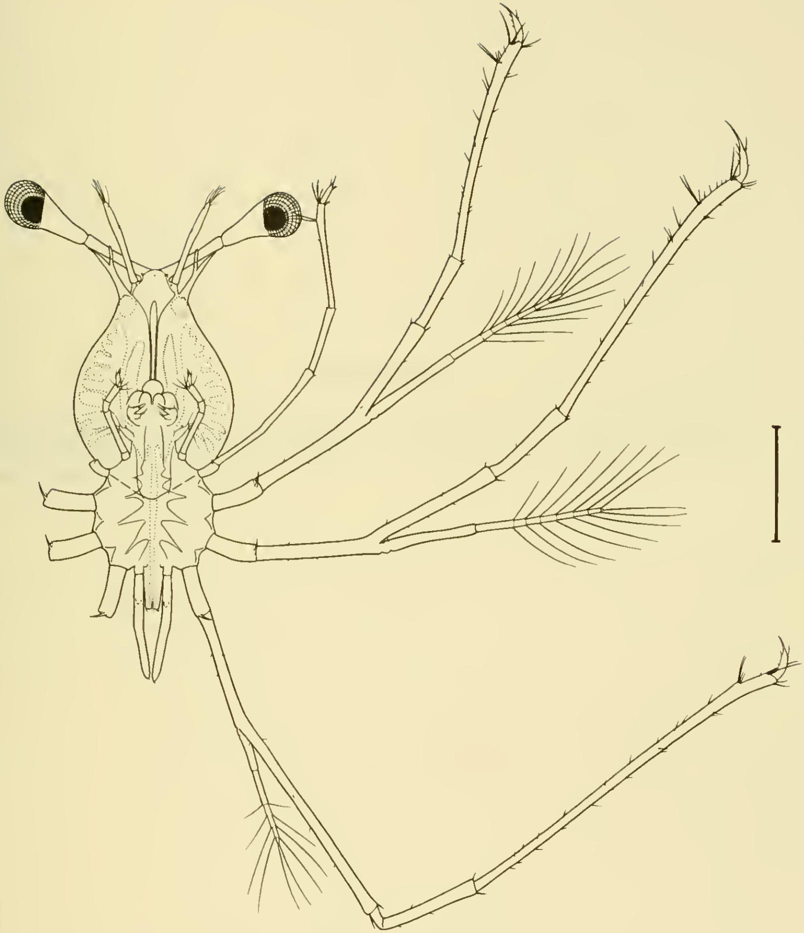


Figure 66

Scyllarides aequinoctialis. Stage IV, reared. Scale represents 1.0 mm.

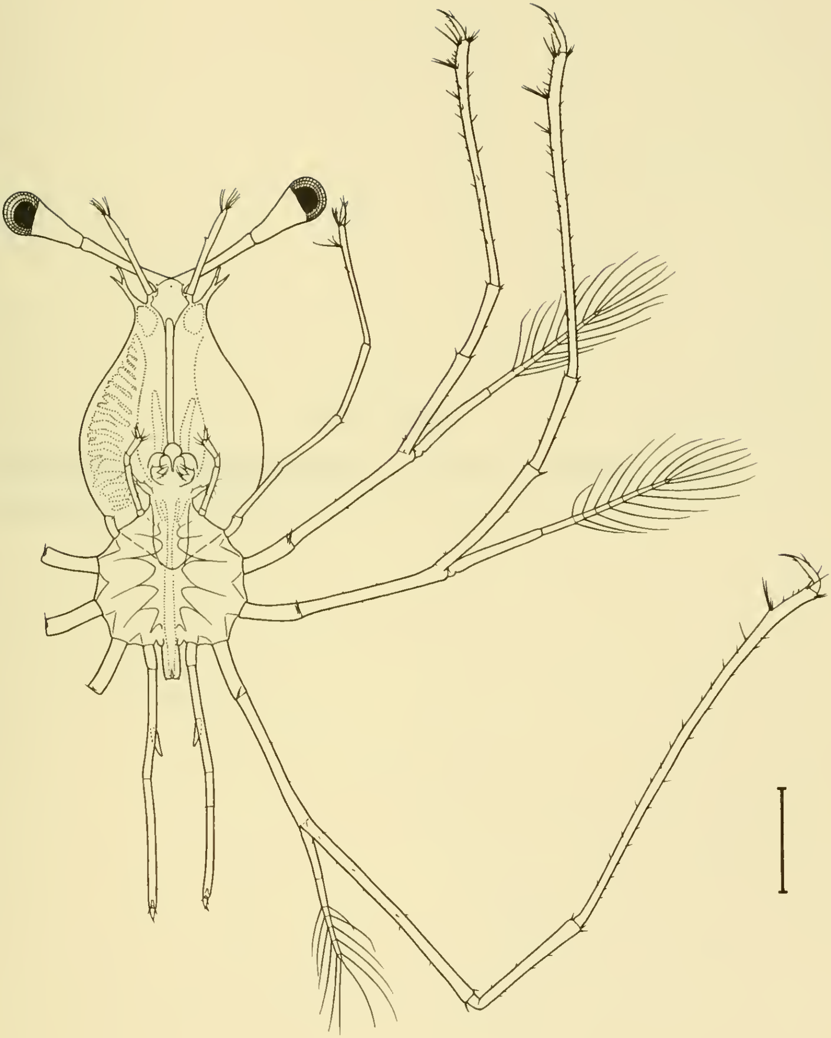


Figure 67

Scyllarides aequinoctialis. Stage V, reared. Scale represents 1.0 mm.

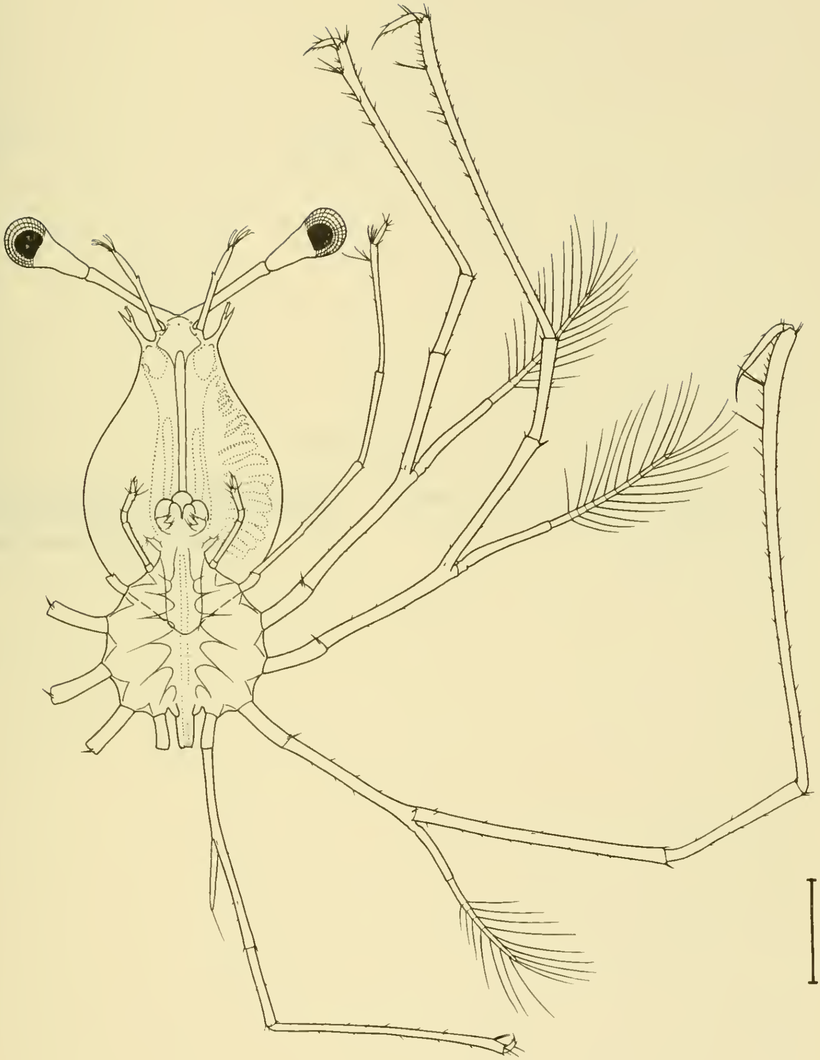


Figure 68

Scyllarides aequinoctialis. Stage VI, reared. Scale represents 1.0 mm.

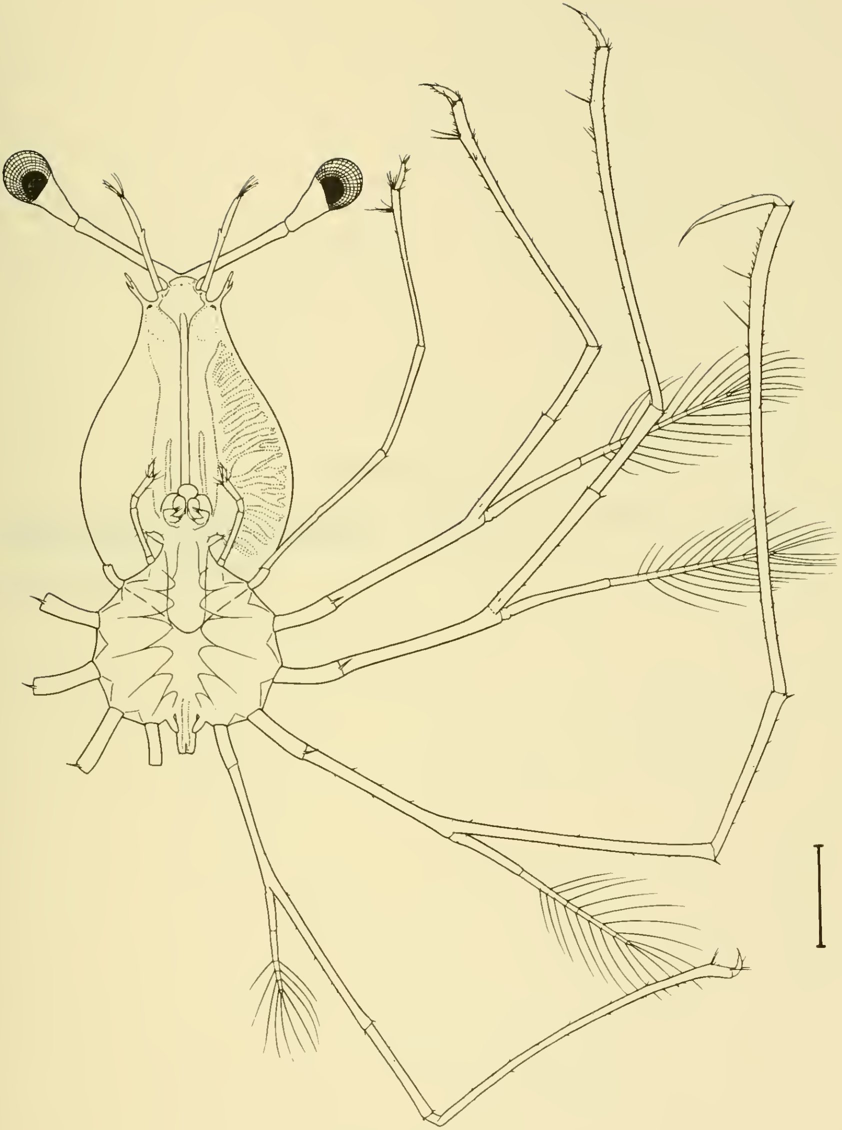


Figure 69

Scyllarides aequinoctialis. Stage VII, reared. Scale represents 1.0 mm.

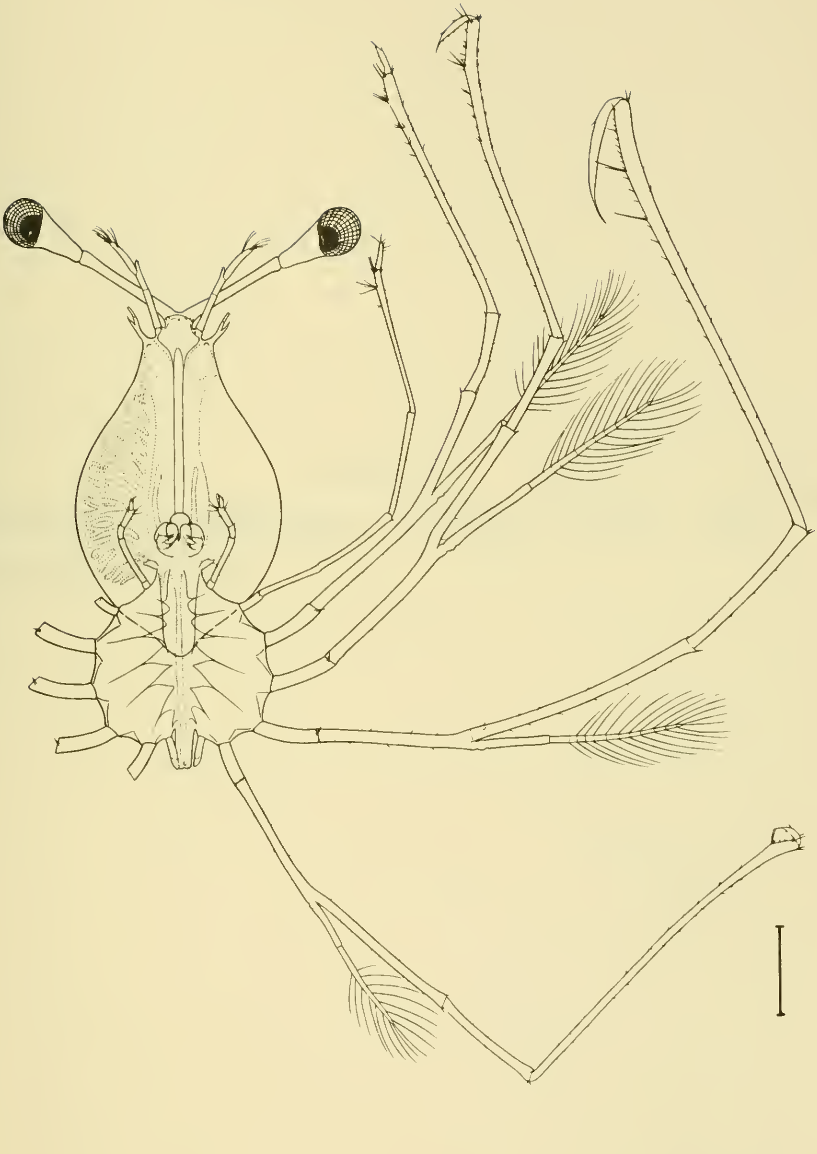


Figure 70

Scyllarides aequinoctialis. Stage VIII, reared. Scale represents 1.0 mm.

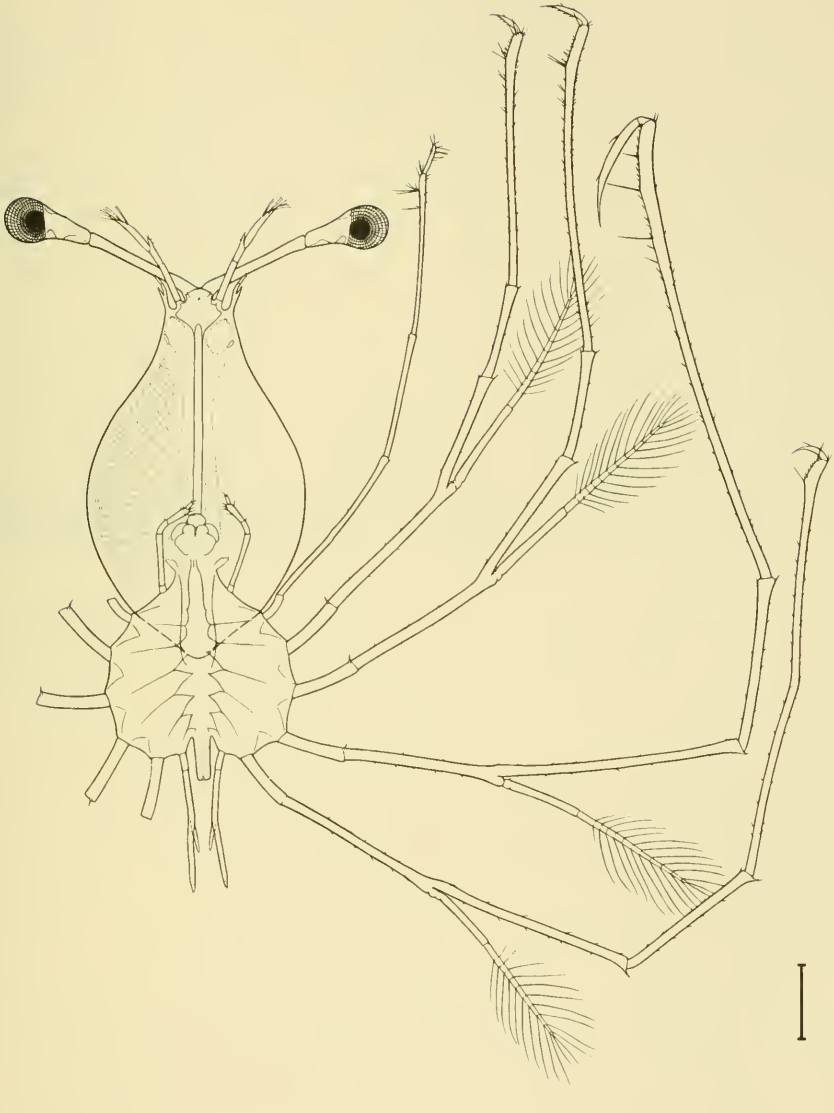


Figure 71

Scyllarides aequinoctialis. 8.3 mm, plankton.

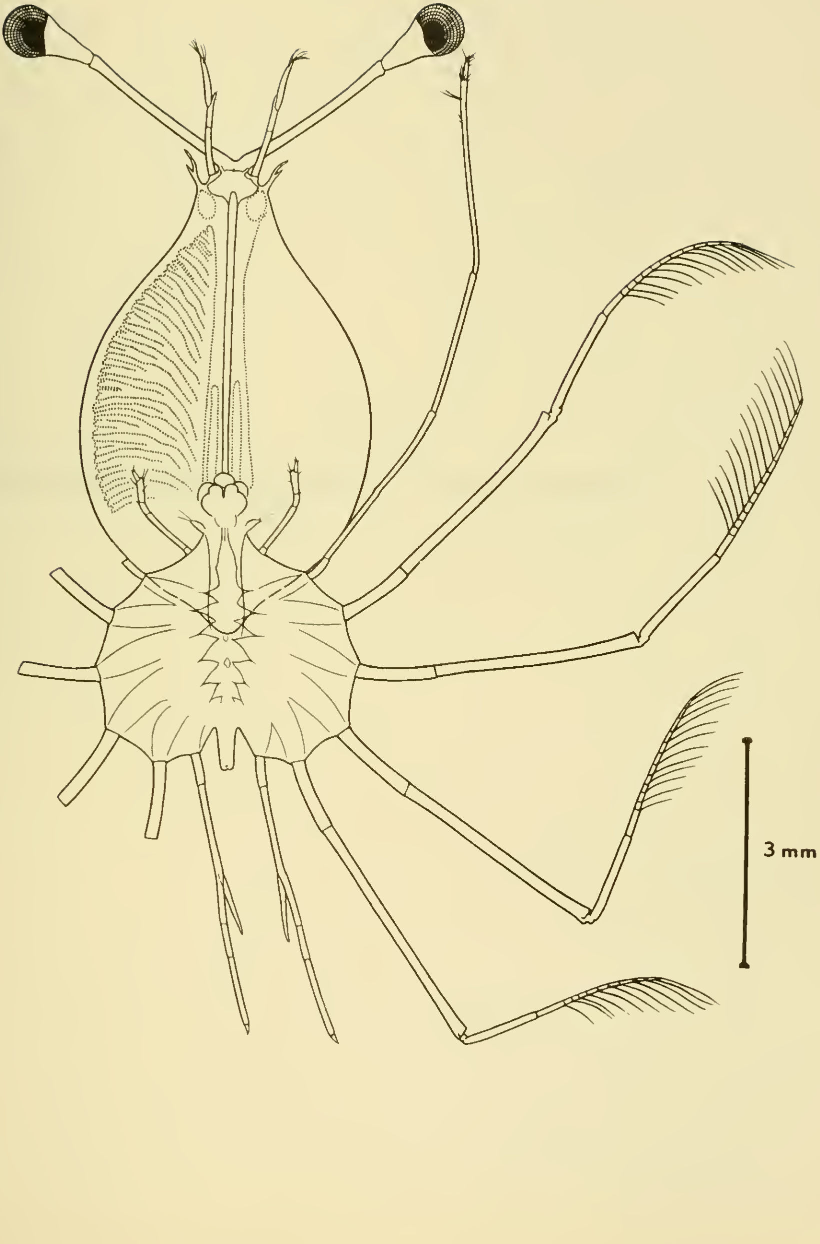

3 mm

Figure 72

Scyllarides aequinoctialis. 8.9 mm, plankton.

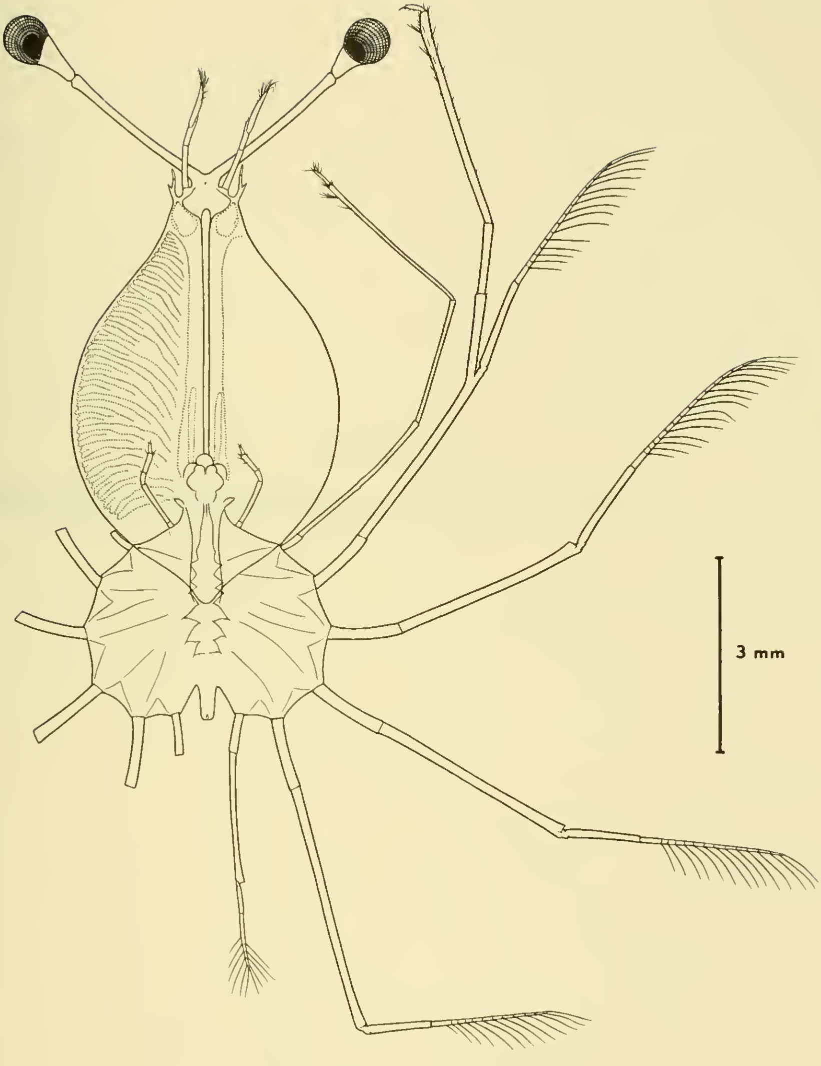

3 mm

Figure 73

Scyllarides aequinoctialis. 13.3 mm, plankton.

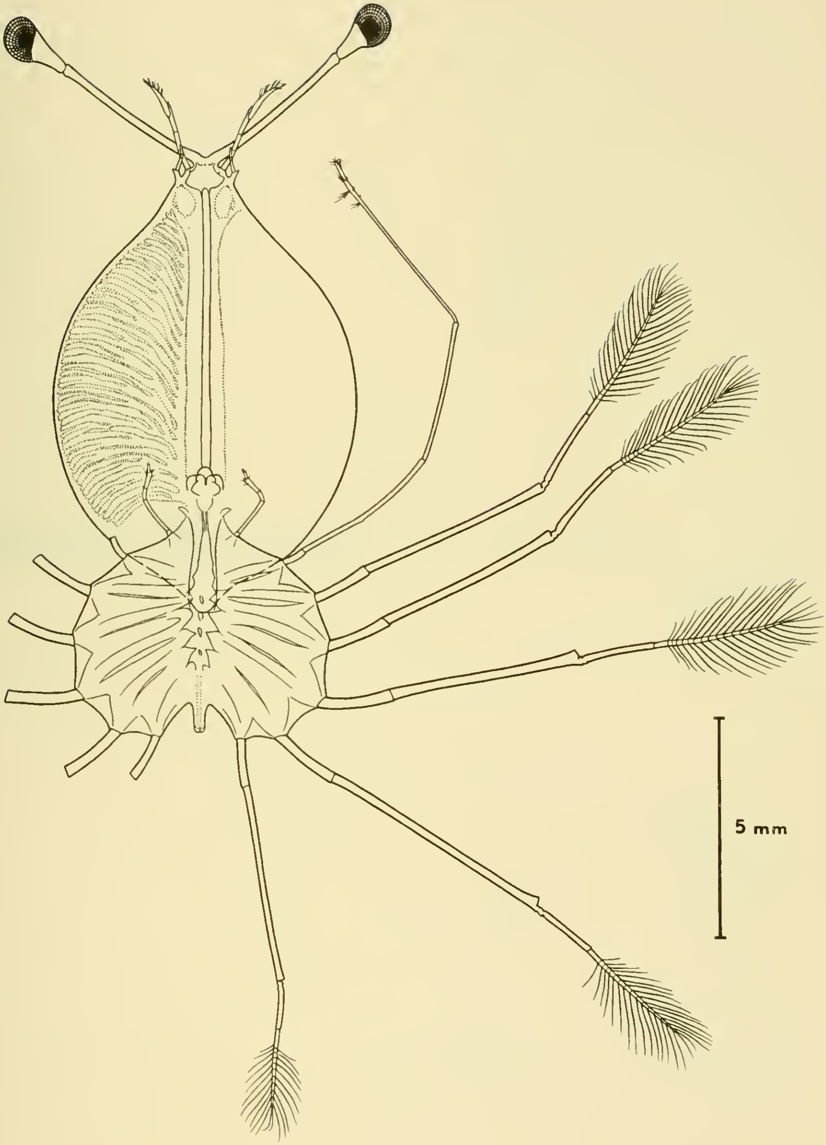

5 mm

Figure 74

Scyllarides aequinoctialis. 16.2 mm, plankton.

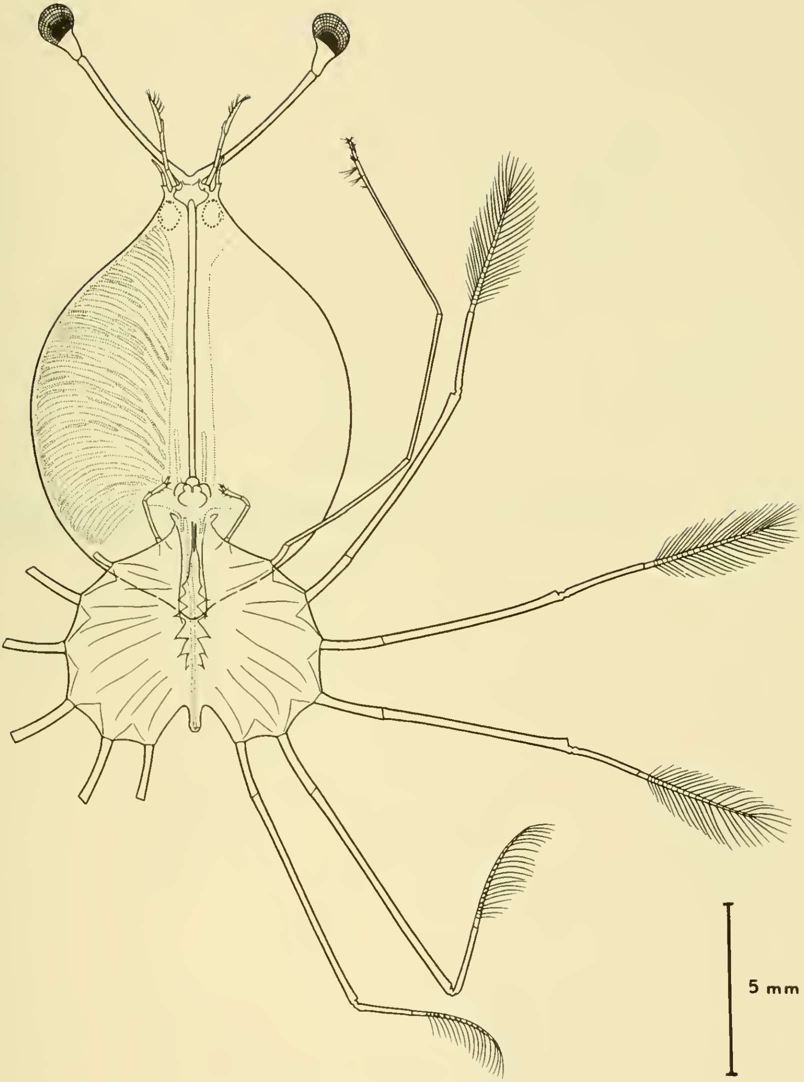

5 mm

Figure 75

Scyllarides aequinoctialis. 22.8 mm, plankton.

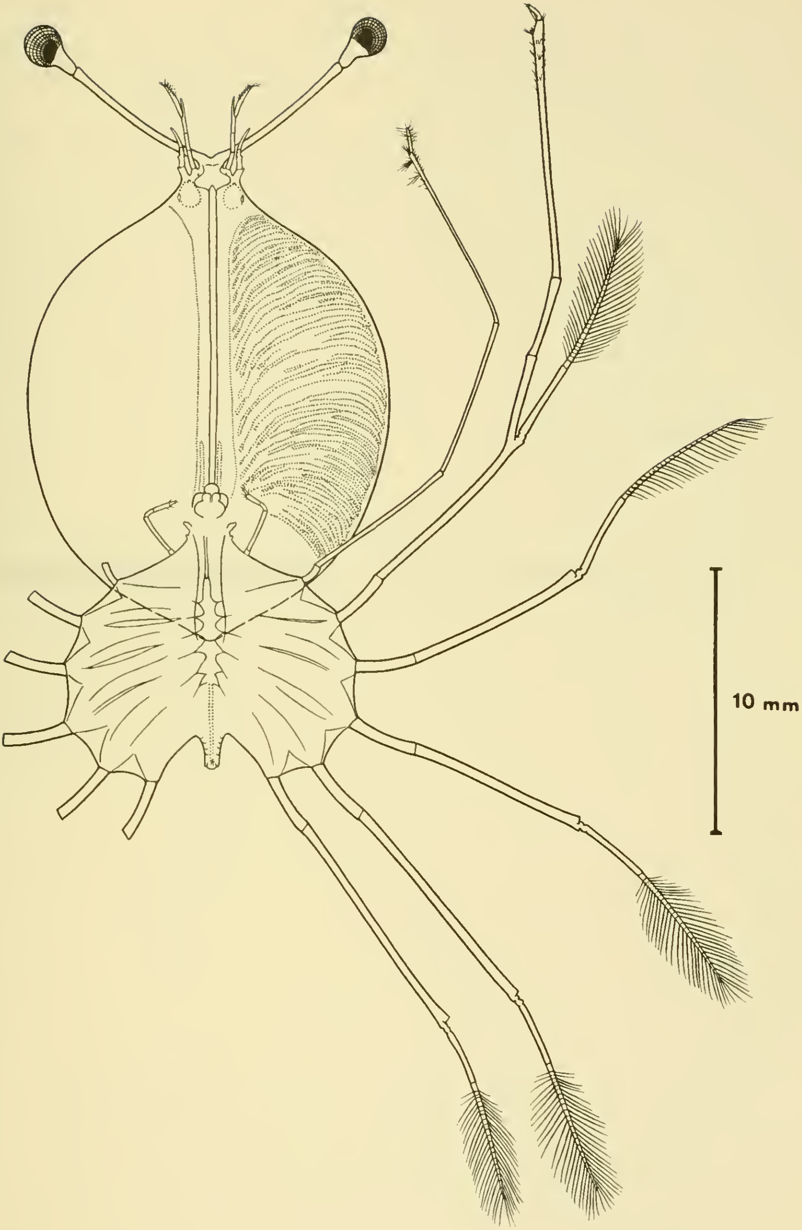
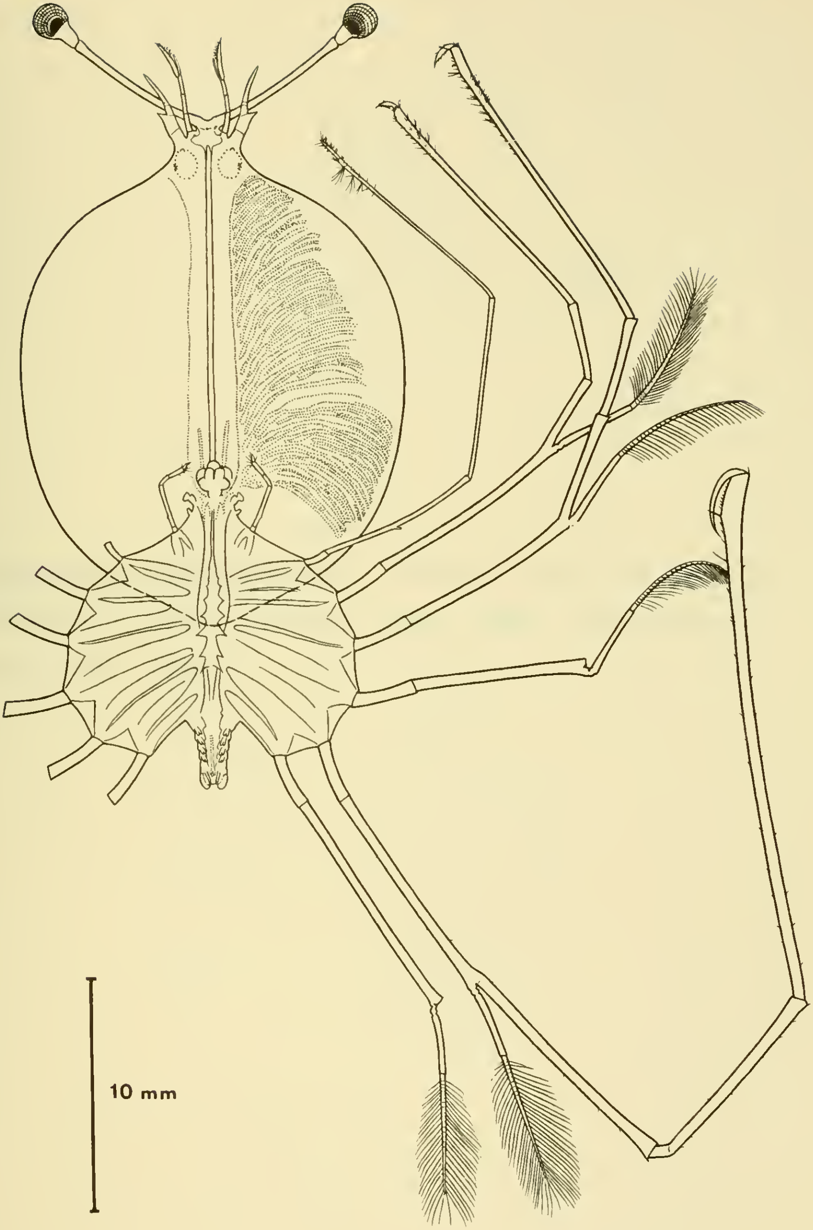

10 mm

Figure 76

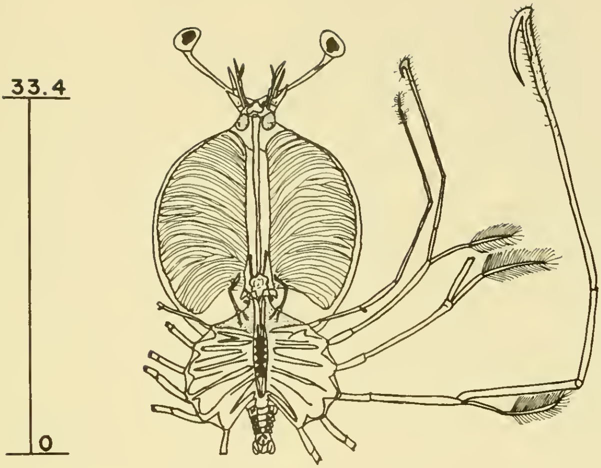
Scyllarides aequinoctialis. 28.8 mm, plankton.



10 mm

Figure 77

Scyllarides aequinoctialis. Subfinal and final stages, plankton. Upper, subfinal stage. Lower, final stage. From Sims, 1965a.


33.4
0

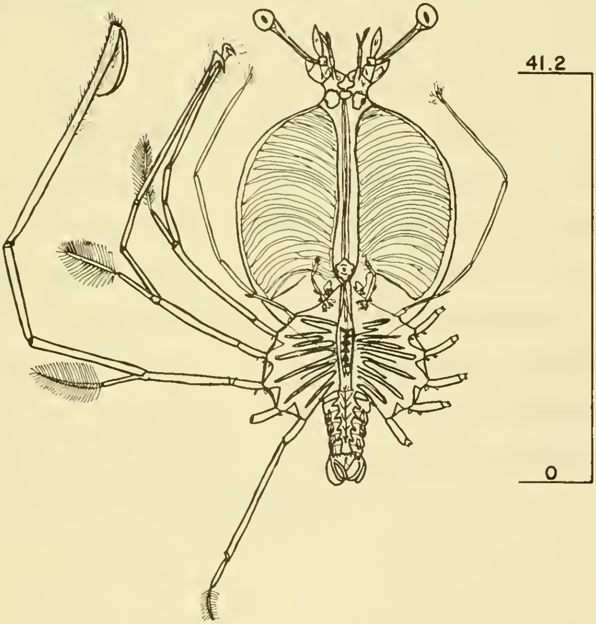

41.2
0

Figure 78

Scyllarides aequinoctialis. Abdomen of phyllosoma stages. A, stage I, reared. B, stage II, reared. C, stage III, reared. D, stage IV, reared. E, stage V, reared. F, stage VI, reared. G, stage VII, reared. H, stage VIII, reared. I, 8.3 mm, plankton. J, 13.3 mm, plankton. K, 16.2 mm, plankton. L, 20.8 mm, plankton. M, 22.8 mm, plankton. N, 24.8 mm, plankton. O, 26.8 mm, plankton. P, 28.8 mm, plankton. Q, "Phyllosome C" (33.4 mm), plankton. R, final stage, plankton (G-350). S, same, outline in lateral view. Scales AB, C-F represent 0.2 mm; scale GHI represents 0.5 mm; scale JK represents 1.0 mm; scale L-P represents 2.0 mm; scale QRS represents 5.0 mm.

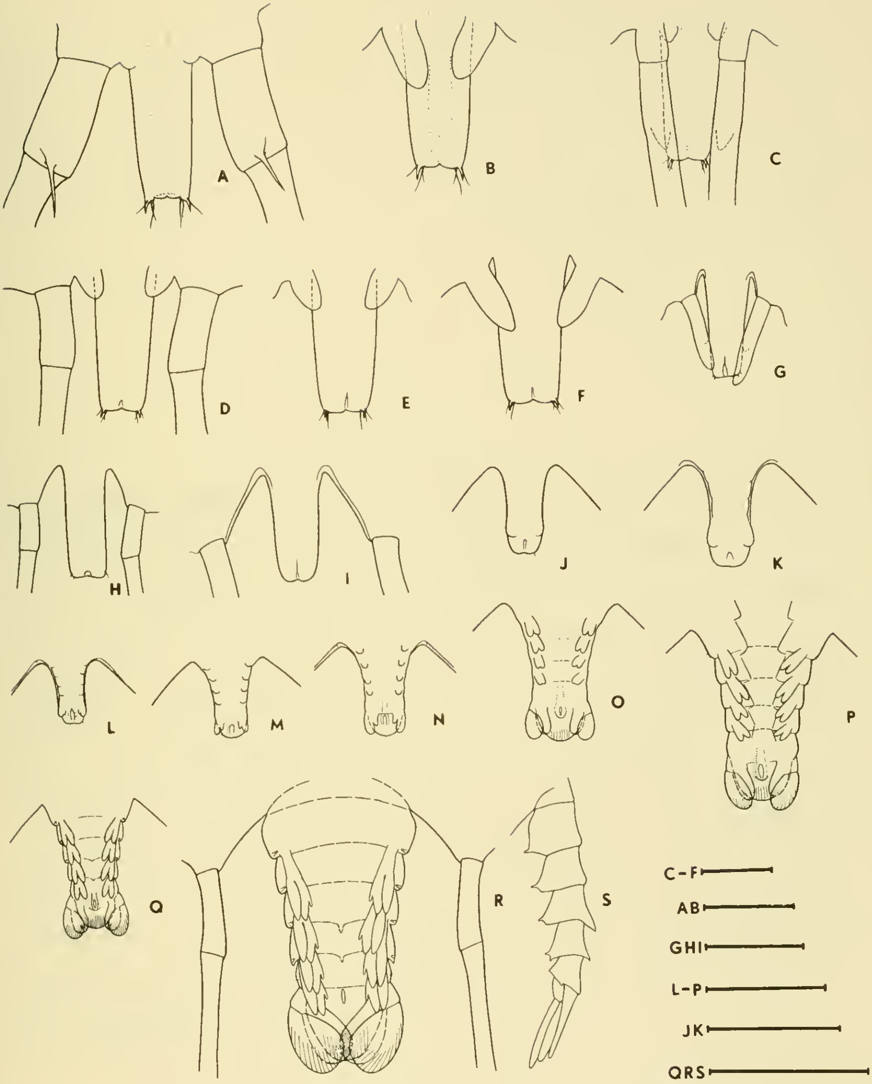

A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
C–F
AB
GHI
L–P
JK
QRS

Figure 79

Scyllarides aequinoctialis. Antennule and antenna of phyllosoma stages. A, stage I, reared. B, stage II, reared. C, stage III, reared. D, stage IV, reared. E, stage V, reared. F, stage VI, reared. G, stage VII, reared. H, stage VIII, reared. I, 8.3 mm, plankton. J, 8.9 mm, plankton. K, 13.3 mm, plankton. L, 16.2 mm, plankton. M, 20.8 mm, plankton. N, 22.8 mm, plankton. O, 24.8 mm, plankton. P, 26.8 mm, plankton. Q, 28.8 mm, plankton. R, "Phyllosome C" (33.4 mm), plankton. S, "Phyllosome B" (41.2 mm), plankton. Scales AB, C-E represent 0.2 mm; scale F-J represents 0.5 mm; scales KL, M-Q represent 1.0 mm; scale RS represents 2.0 mm.

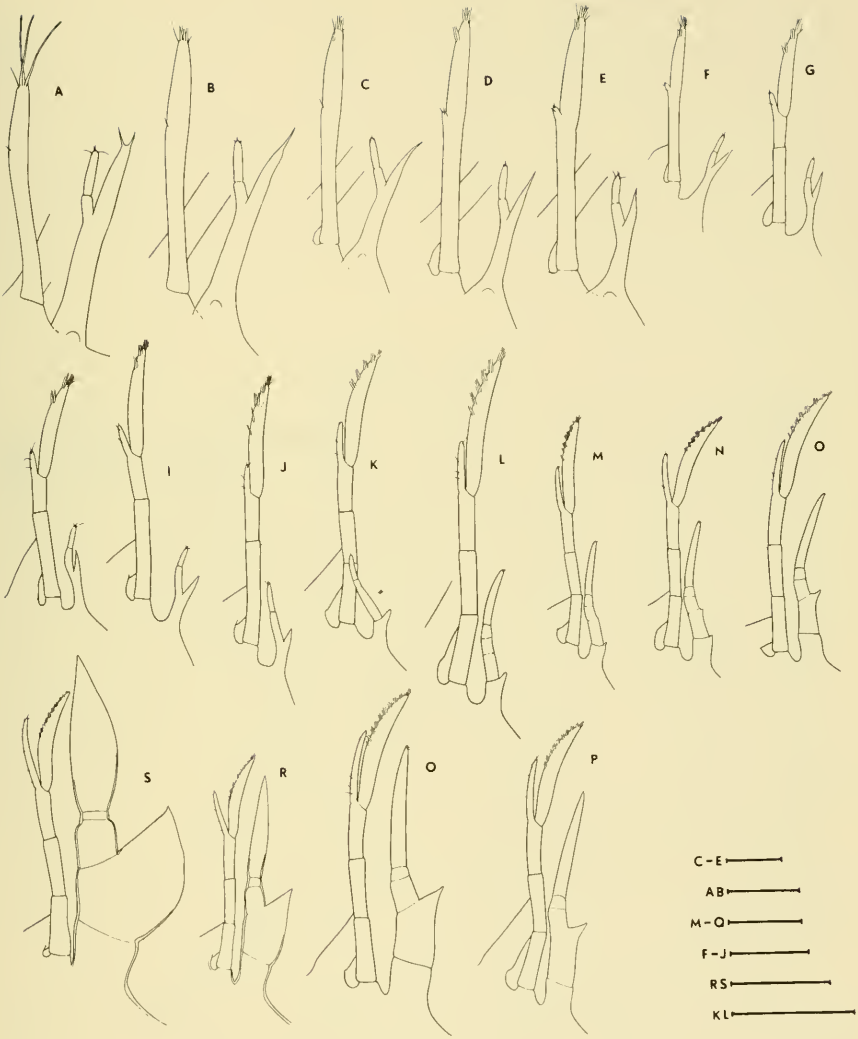

A
B
C
D
E
F
G
I
J
K
L
M
N
O
S
R
O
P
C – E
AB
M – Q
F – J
RS
KL

Figure 80

Scyllarides aequinoctialis. Maxilla 2 and maxillipeds of phyllosoma stages. A, maxilla 2 and maxilliped 2, stage I, reared. B, maxilla 2, stage VIII, reared. C, maxilla 2, 8.3 mm, plankton. D, maxilla 2, 8.9 mm, plankton. E, maxilla 2 and maxilliped 1, 13.3 mm, plankton. F, same, 16.2 mm, plankton. G, same, 20.8 mm, plankton. H, same, 22.8 mm, plankton. I, same, 24.8 mm, plankton. J, same, 26.8 mm, plankton. K, same, 28.8 mm, plankton. L, same, "Phyllosome C" (33.4 mm), plankton. M, maxilla 2, maxilliped 1 and maxilliped 2, final stage, plankton (G-350). N, proximal portion of maxilliped 2, "Phyllosome C." O, maxilliped 2, 28.8 mm, plankton. P, distal portion of maxilliped 3, stage I, reared. Q, exopod bud of maxilliped 3, "Phyllosome C." R, same, final stage (G-350). Scales A-F, P represent 0.2 mm; scale G-L represents 0.5 mm; scale MNOQR represents 1.0 mm.

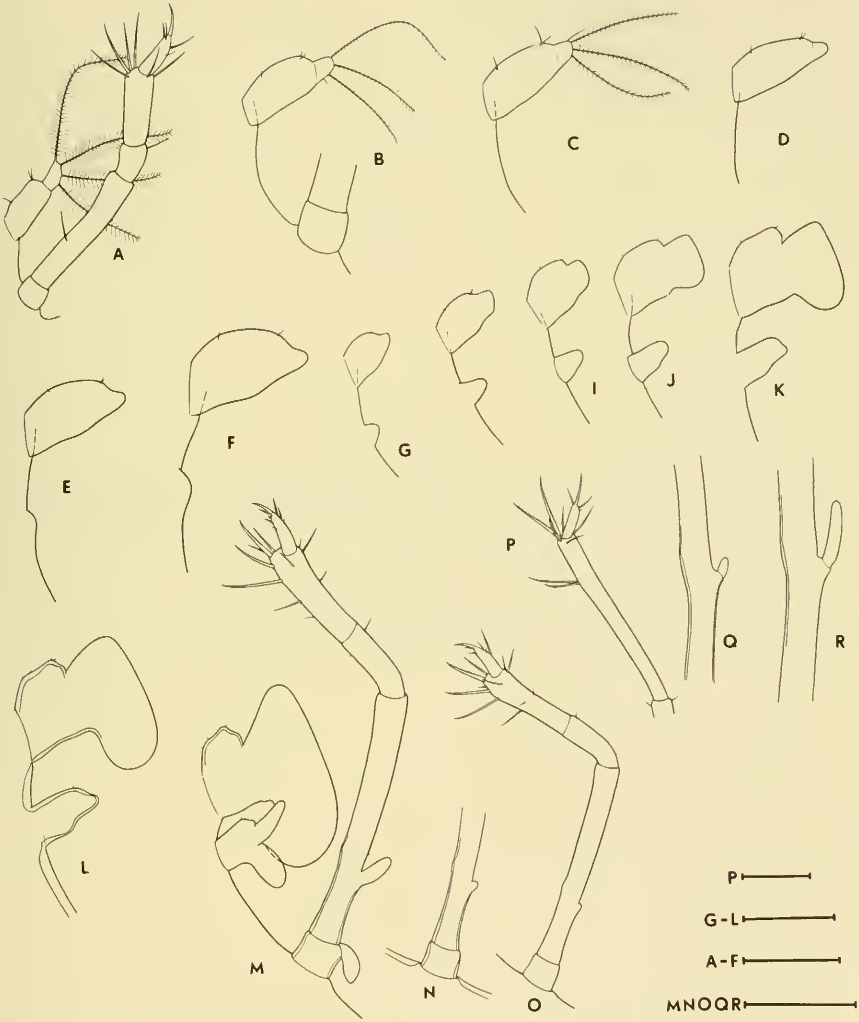

A
B
C
D
E
F
G
I
J
K
L
M
N
O
P
Q
R
P
G-L
A-F
MNOQR

Figure 81

Scyllarides aequinoctialis. Maxilla 1 of phyllosoma stages. A, stage I, reared. B, stage V, reared. C, stage VIII, reared. D, 8.3 mm, plankton. E, final stage, plankton (G-350). Scale A-D represents 0.2 mm; scale E represents 0.5 mm.

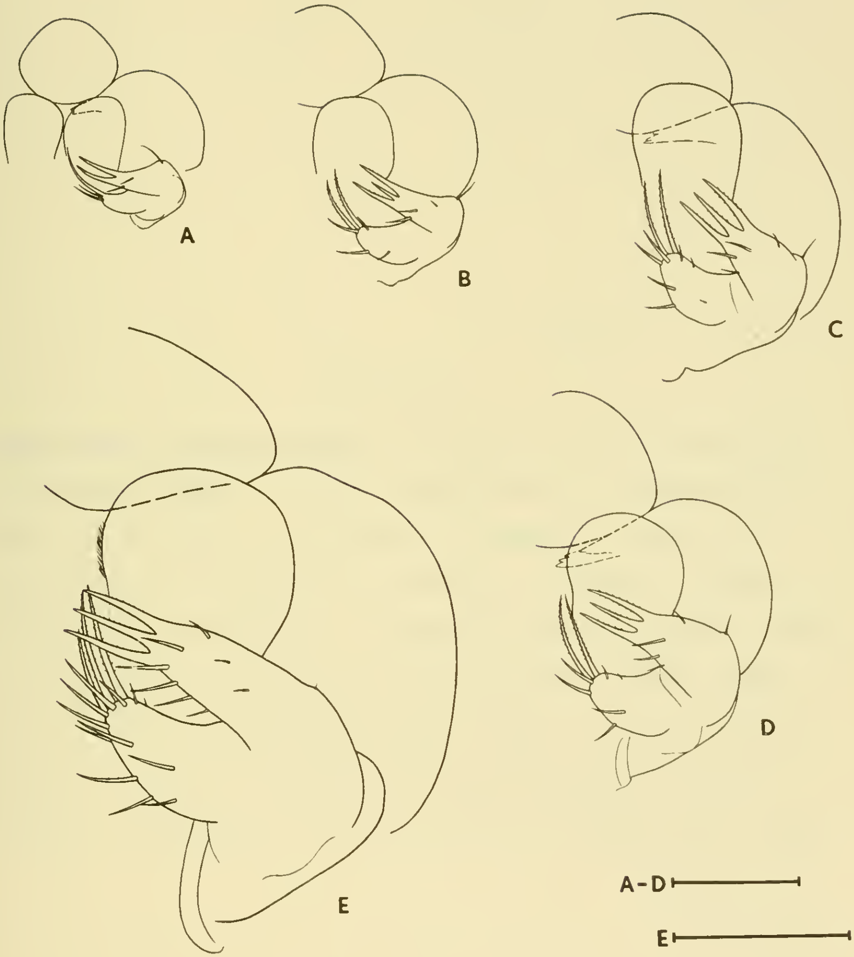

A
B
C
D
E
A-D
E

Figure 82

Scyllarides aequinoctialis. Distal end of pereiopods of phyllosoma stages. A, B, C: pereiopods 1-3 respectively, stage I, reared. D, pereiopod 3, stage IV, reared. E, same, stage V, reared. F, pereiopod 4, stage V, reared. G, H, I, J: pereiopods 1-4 respectively, stage VIII, reared. K, L, M, N, O: pereiopods 1-5 respectively, final stage. K, L, M, N from final phyllosoma, G-350; O from "Phyllosome B" (41.2 mm). Scales ABC, DEF represent 0.2 mm; scale G-J represents 1.0 mm; scale K-O represents 3.0 mm.

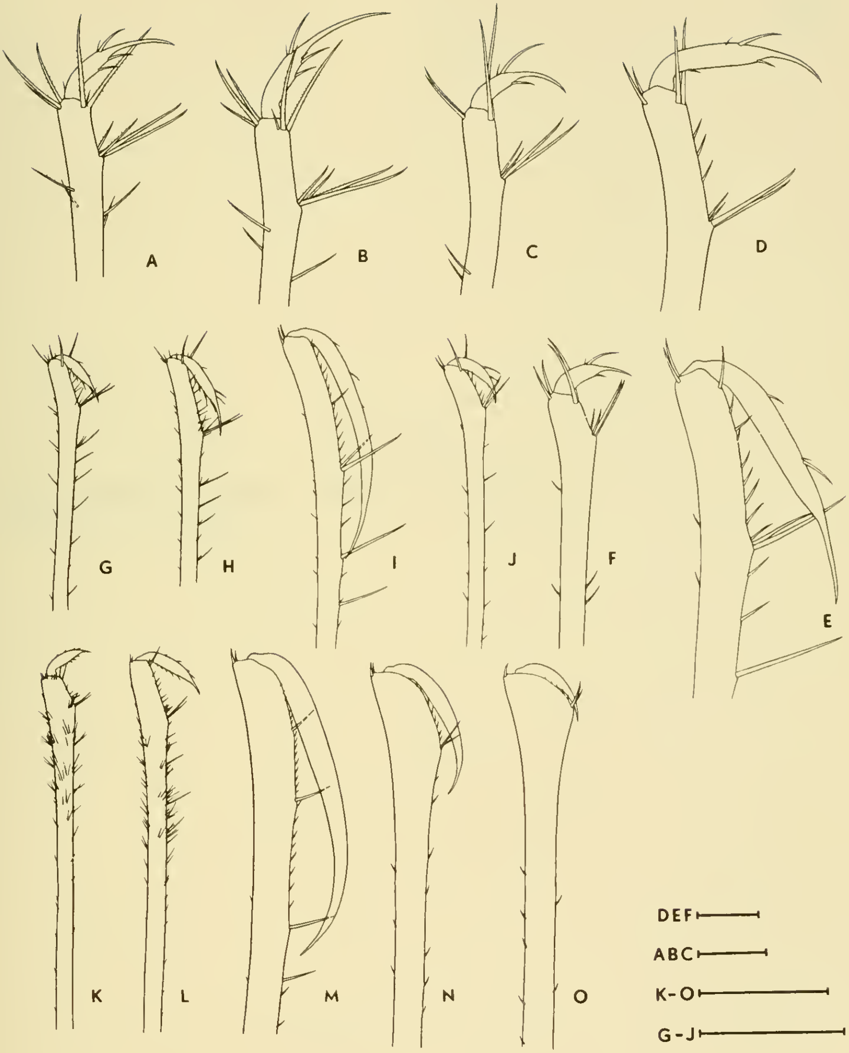

A
B
C
D
G
H
I
J
F
E
K
L
M
N
O
DEF
ABC
K-O
G-J

Figure 83

Scyllarides *nodifer*. 6.6 mm, plankton.

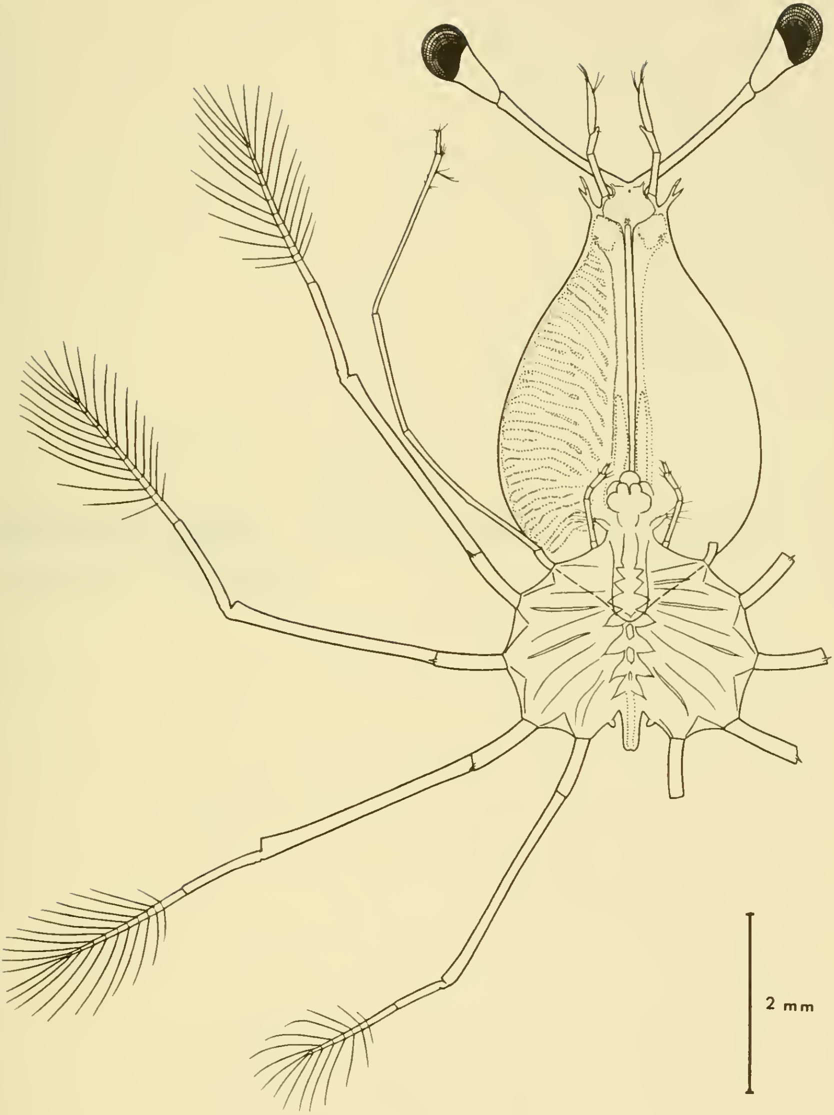

2 mm

Figure 84

Scyllarides nodifer. 12.8 mm, plankton. The dactyl of pereiopod 3 is missing.

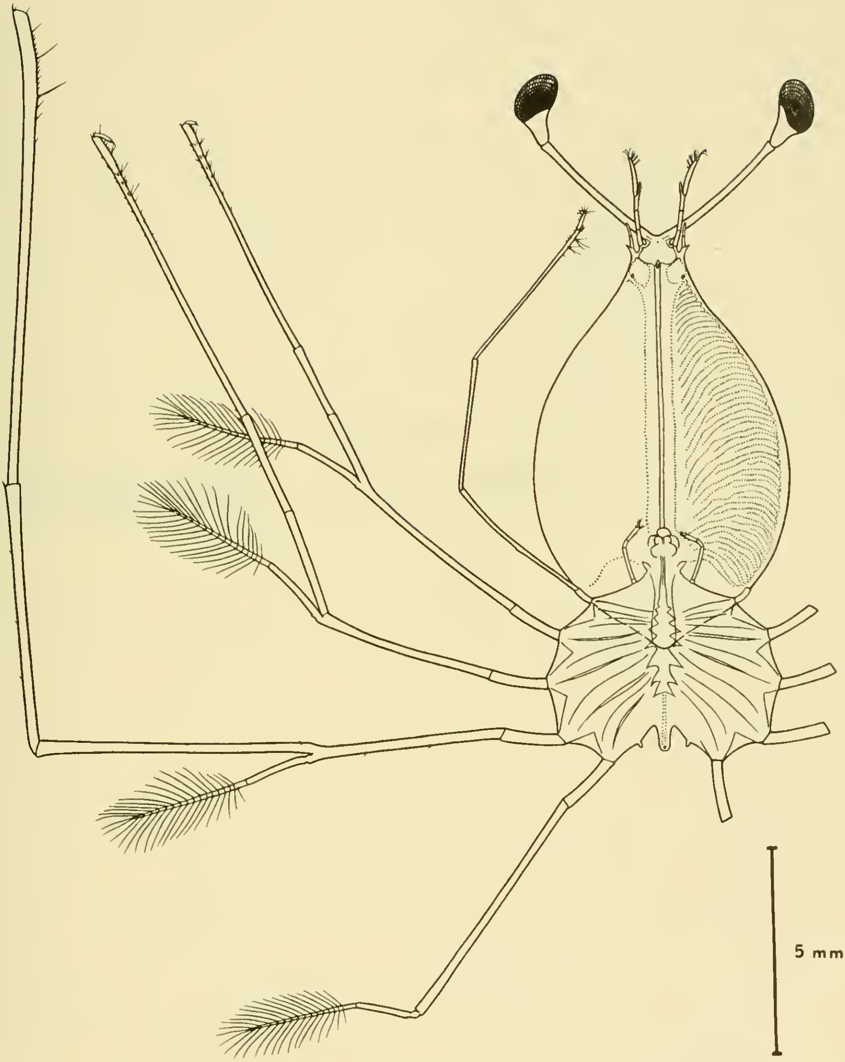

5 mm

Figure 85

Scyllarides nodifer. 18.4 mm, plankton.

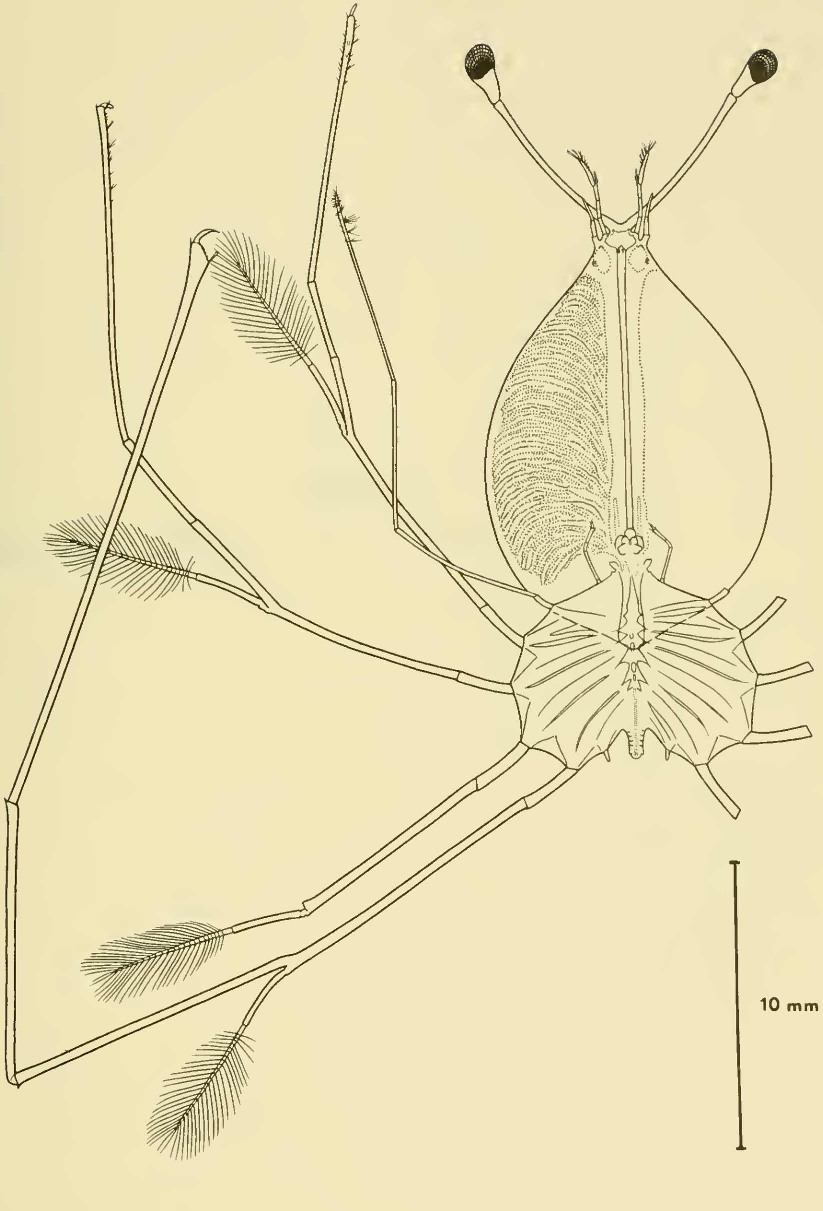

10 mm

Figure 86

Scyllarides nodifer. 26.6 mm, plankton.

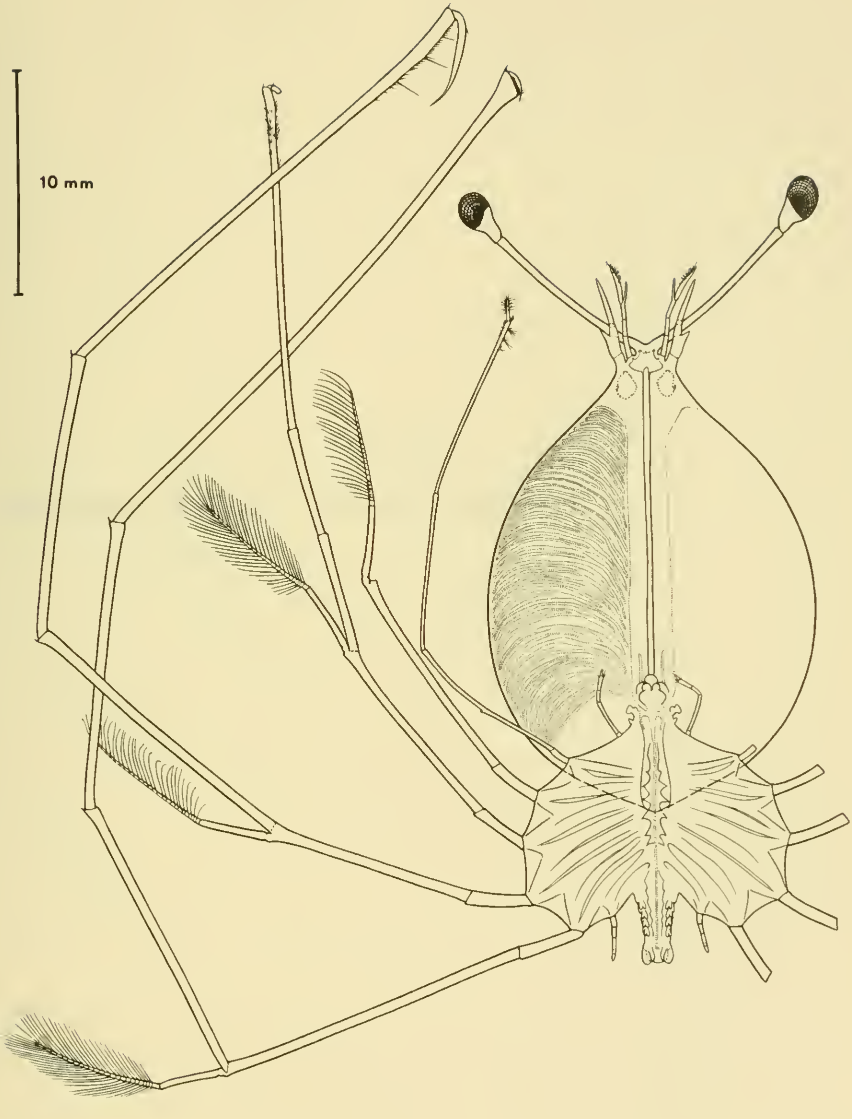

10 mm

Figure 87

Scyllarides nodifer. 30.2 mm, plankton.

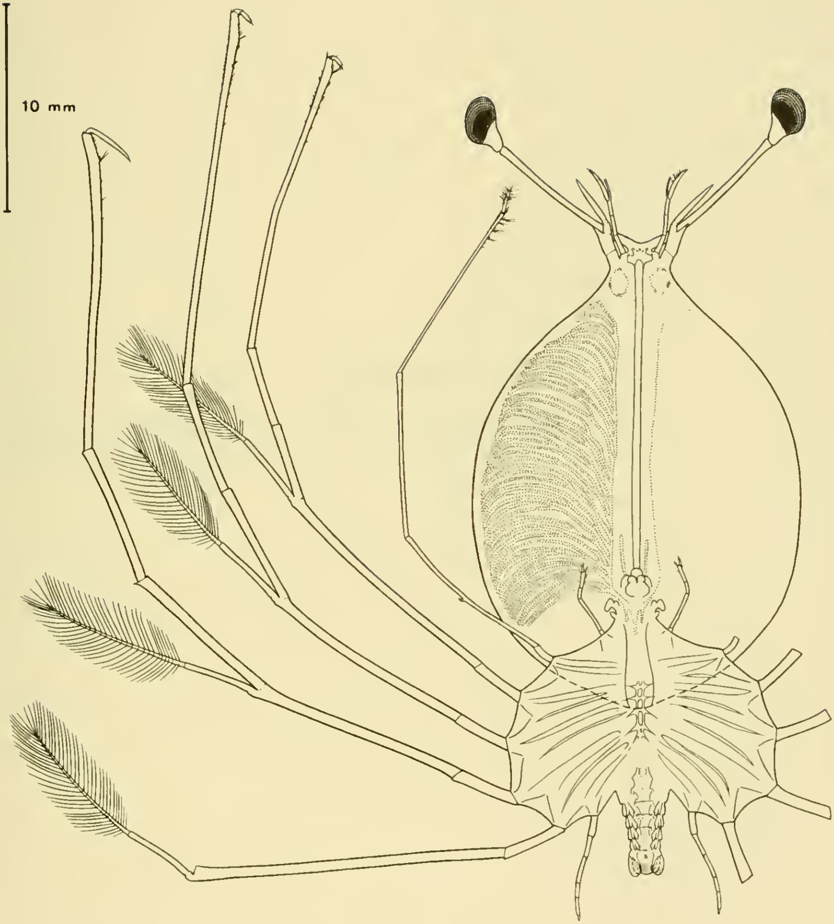

10 mm

Figure 88

Scyllarides nodifer. 36.7 mm, plankton.

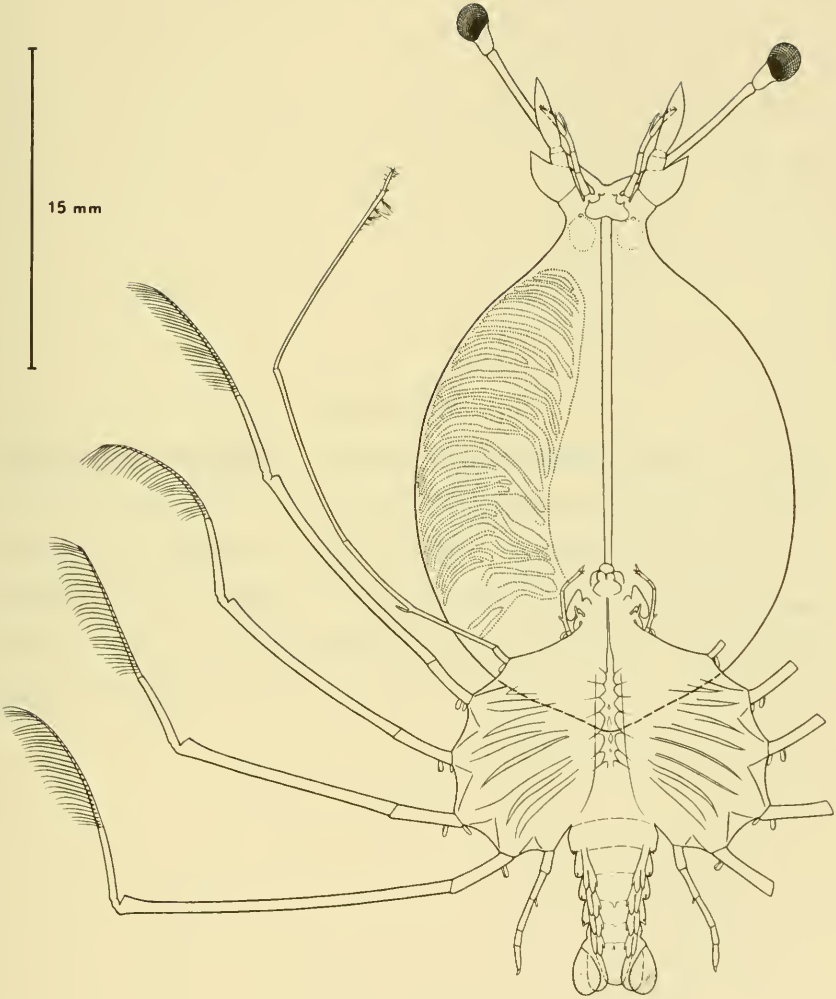

15 mm

Figure 89

Scyllarides nodifer. Abdomen of phyllosoma stages. A, 6.6 mm. B, 12.8 mm. C, 15.3 mm. D, 18.4 mm. E, 21.0 mm. F, 26.6 mm. G, 30.2 mm. H, 36.7 mm. I, same, outline in lateral view. Scales A, B represent 0.5 mm; scale CD represents 1.0 mm; scale EFG represents 2.0 mm; scale HI represents 4.0 mm.

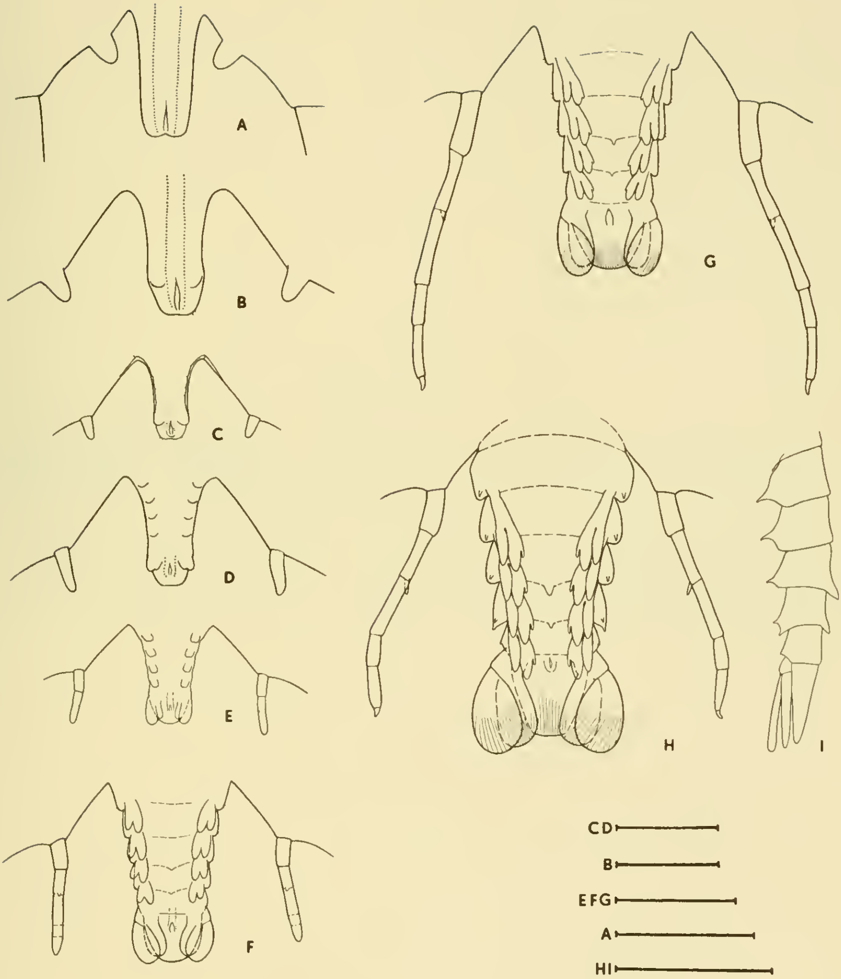

A
B
C
D
E
F
G
H
I
CD
B
EFG
A
HI

Figure 90

Scyllarides nodifer. Antennule and antenna of phyllosoma stages. A, 6.6 mm. B, 12.8 mm. C, 15.3 mm. D, 18.4 mm. E, 21.0 mm. F, 26.6 mm. G, 30.2 mm. H, 36.7 mm. Scales A, B represent 0.5 mm; scales CD, EFG, H represent 1.0 mm.

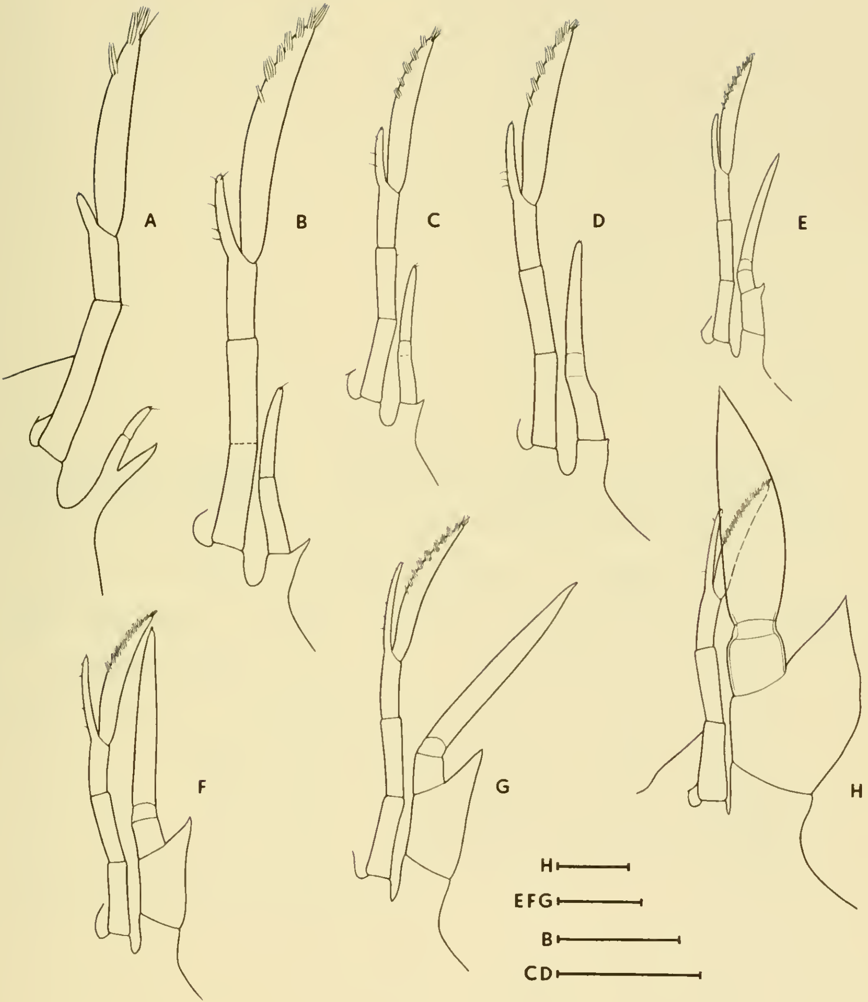

A
B
C
D
E
F
G
H
H
EFG
B
CD
A

Figure 91

Scyllarides nodifer. Appendages of phyllosoma stages. A, maxilla 2, 6.6 mm. B, maxilla 2 and maxilliped 1, 12.8 mm. C, same, 15.3 mm. D, same, 18.4 mm. E, same, 21.0 mm. F, same, 26.6 mm. G, same, 30.2 mm. H, maxilla 2, maxilliped 1 and maxilliped 2, 36.7 mm. I, maxilliped 2, 30.2 mm. J, same, 6.6 mm. K, maxilla 1, 36.7 mm. L, same, 6.6 mm. M, N, O, P: distal end of pereiopods 1-4 respectively, final stage. Scales AB, J, L represent 0.2 mm; scales C-G, K represent 0.5 mm; scales H, I represent 1.0 mm; scale M-P represents 3.0 mm.

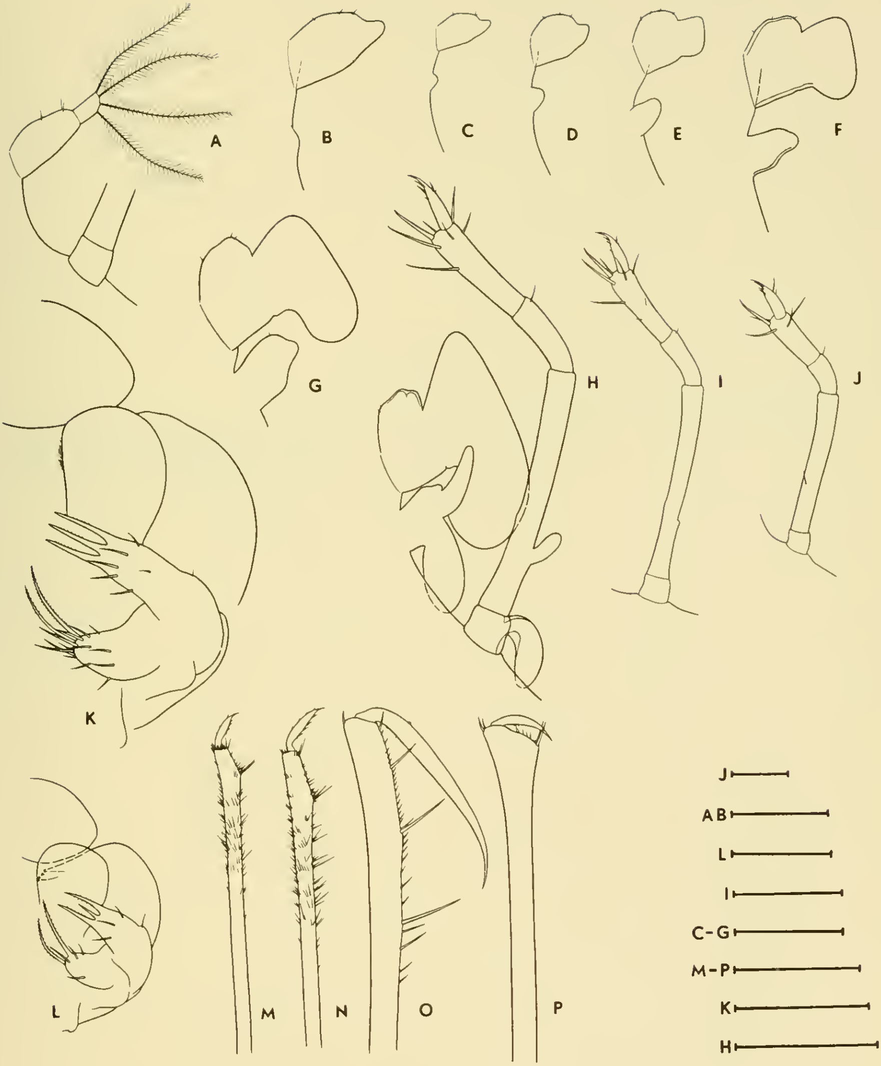

A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
J
AB
L
I
C-G
M-P
K
H

Figure 92

Parribacus antarcticus. 8.5 mm, plankton. The exopod bud of the right fifth leg is broken off.

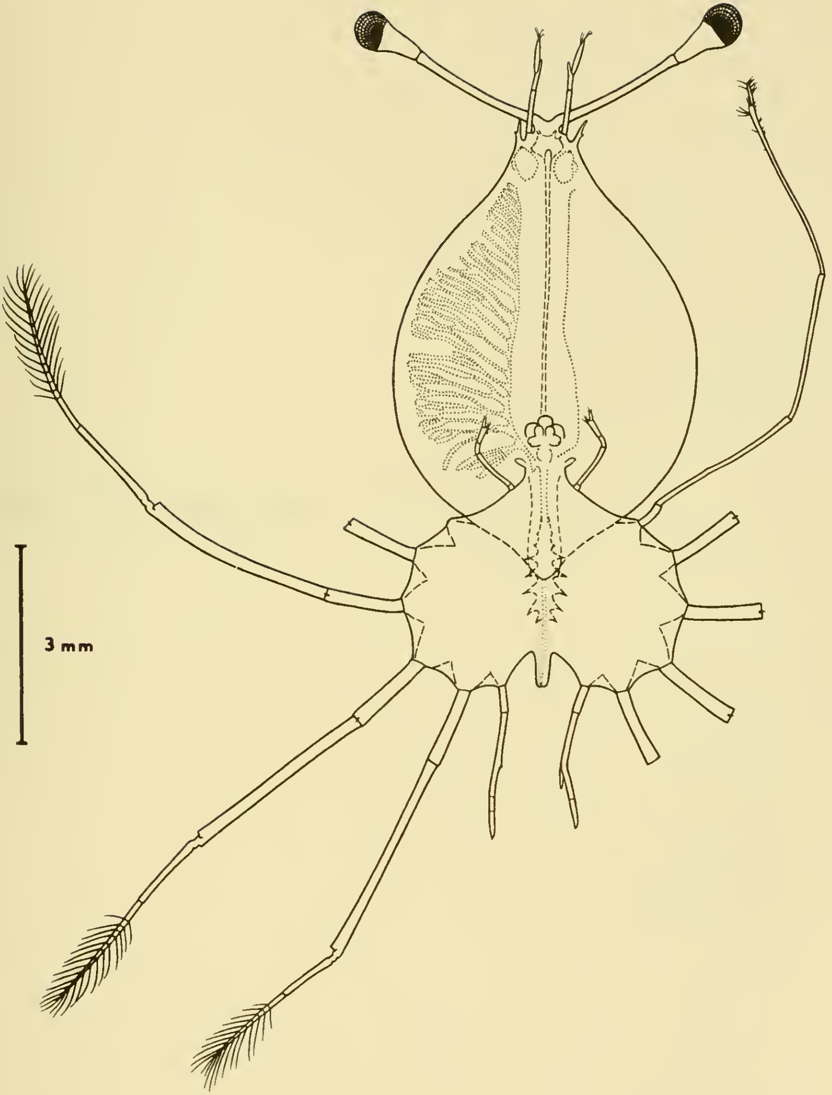

3 mm

Figure 93

Parribacus antarcticus. 13 mm, plankton.

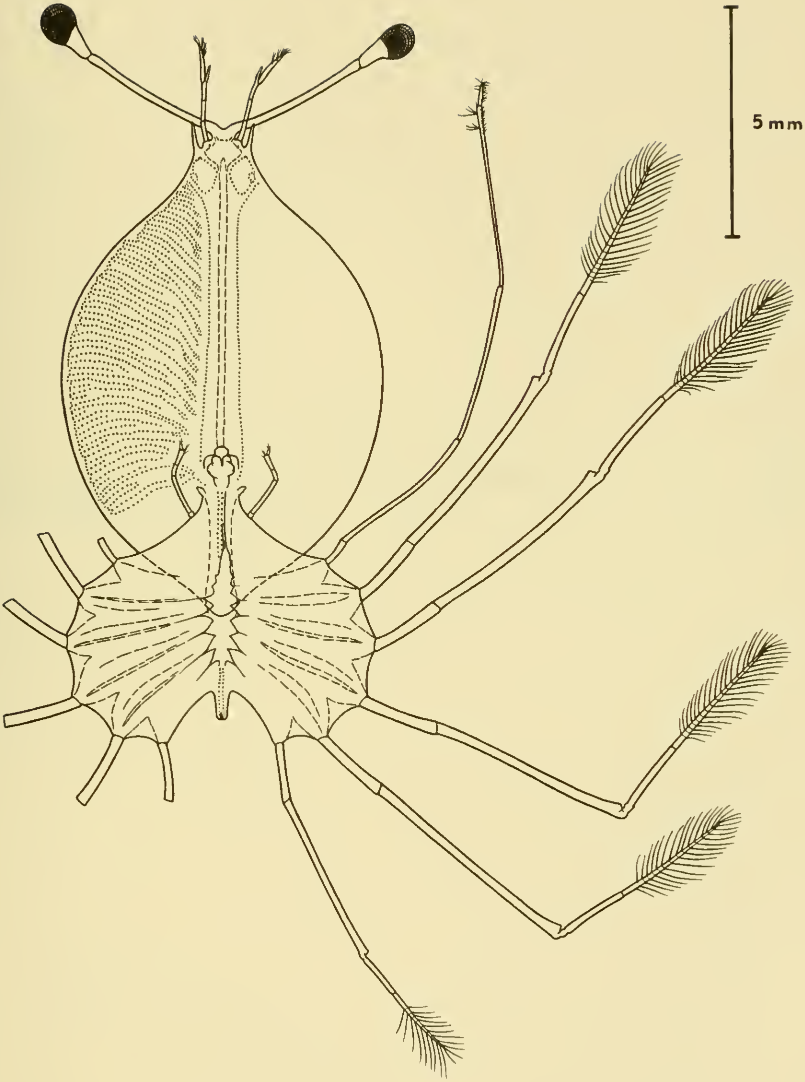

5 mm

Figure 94

Parribacus antarcticus. 24 mm, plankton.

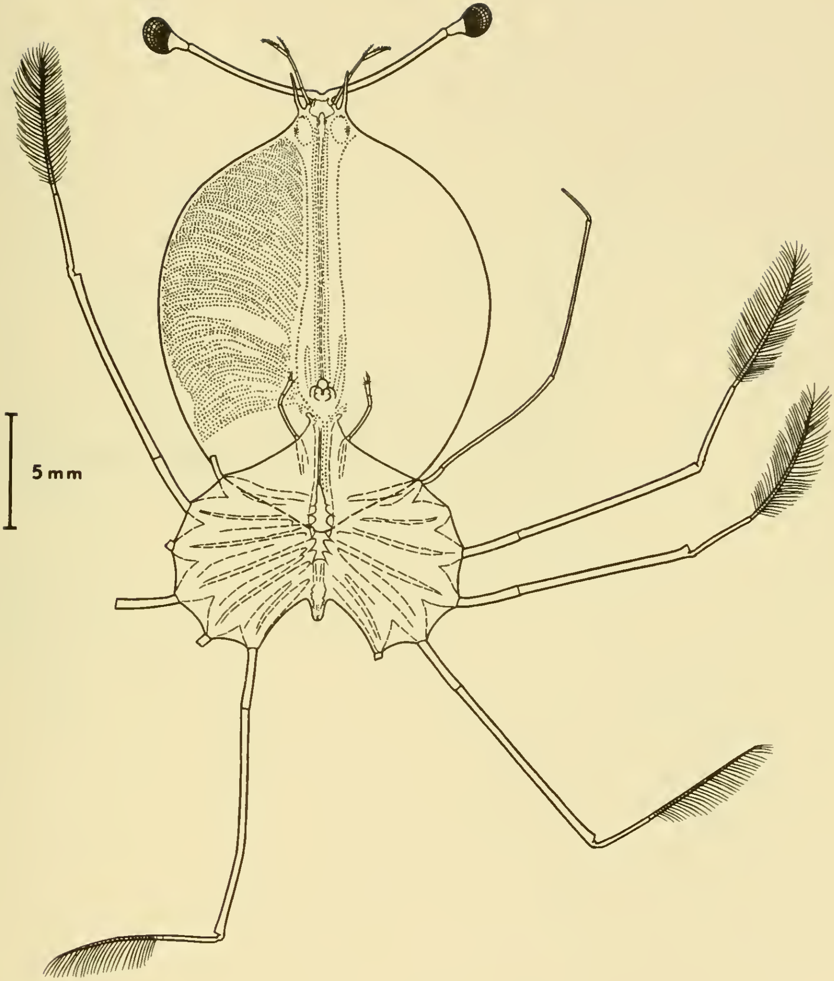

5 mm

Figure 95

Parribacus antarcticus. 65 mm, plankton.

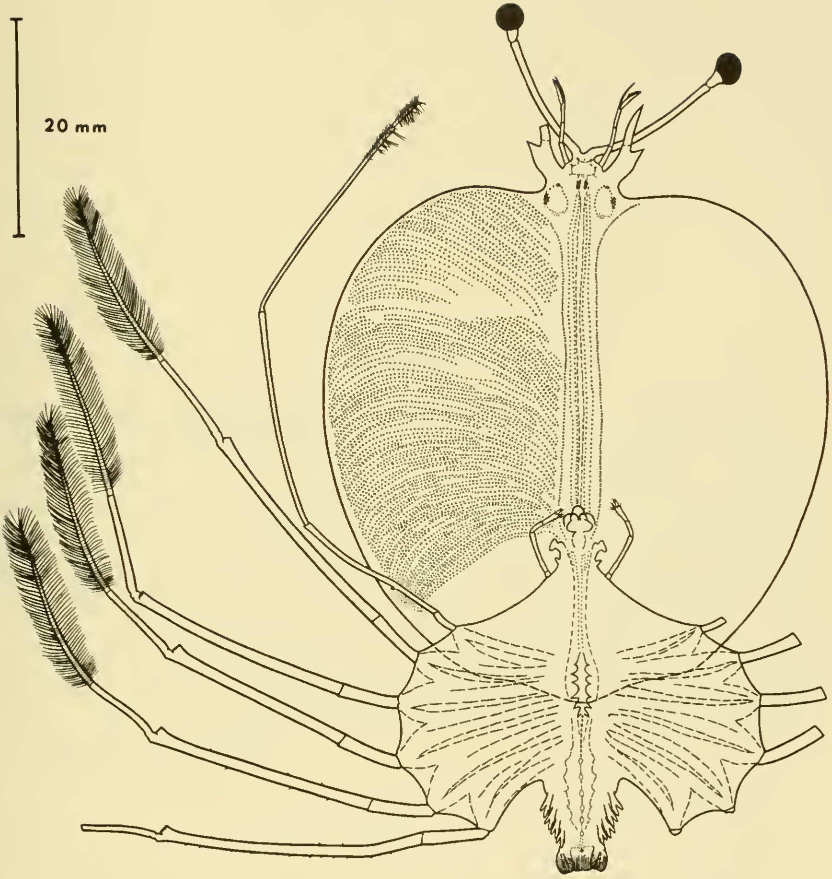

20 mm

Figure 96

Parribacus antarcticus. Appendages of 8.5- and 13-mm phyllosomas. A, C, E, F, H: maxilla 1, maxilla 2, antennule and antenna, maxilliped 2 and abdomen, 8.5-mm phyllosoma. B, D, G, I, J: maxilla 1, maxilla 2, maxilliped 2, abdomen and antennule and antenna, 13-mm phyllosoma. One of the two terminal teeth of the basal endite of A is broken off. Scales A, B, CD represent 0.2 mm; scales E through J represent 0.5 mm.

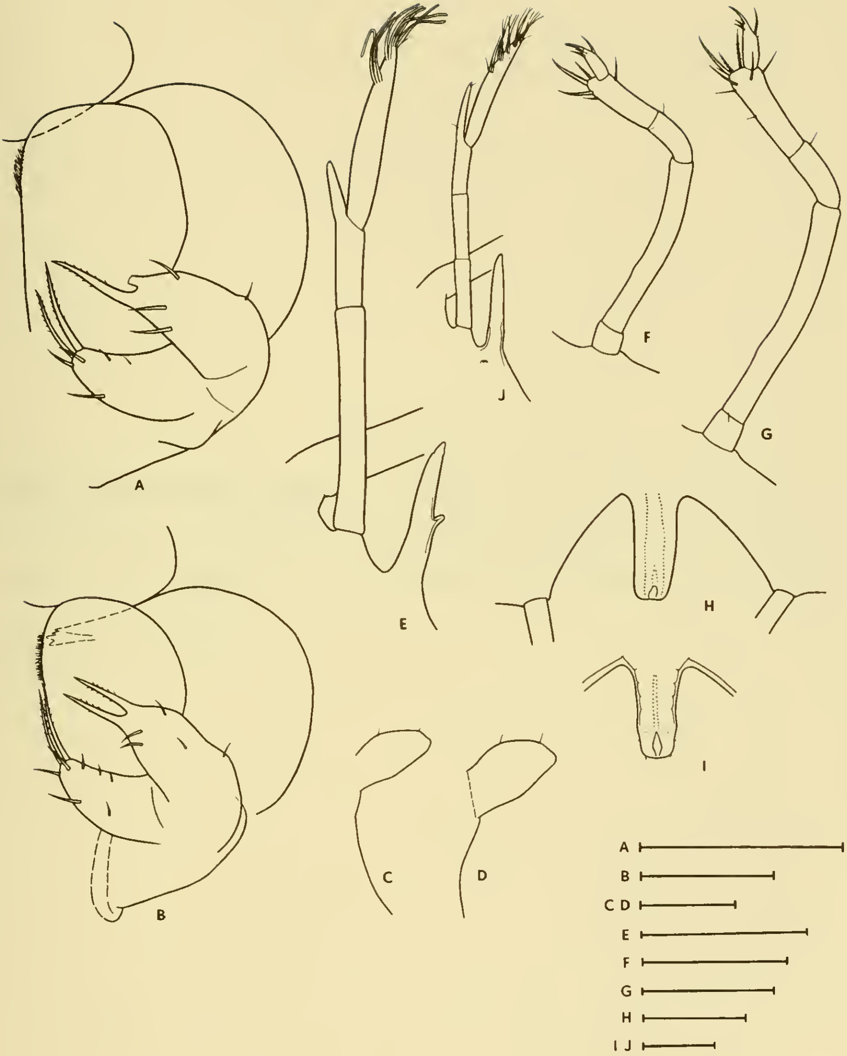

A
B
C
D
E
F
G
H
I
J
A
B
C D
E
F
G
H
I J

Figure 97

Parribacus antarcticus. Appendages of 24-mm phyllosoma. A, maxilla 1. B, maxilla 2 and maxilliped 1. C, maxilliped 2. D, abdomen. E, antennule and antenna. All scales represent 0.5 mm.

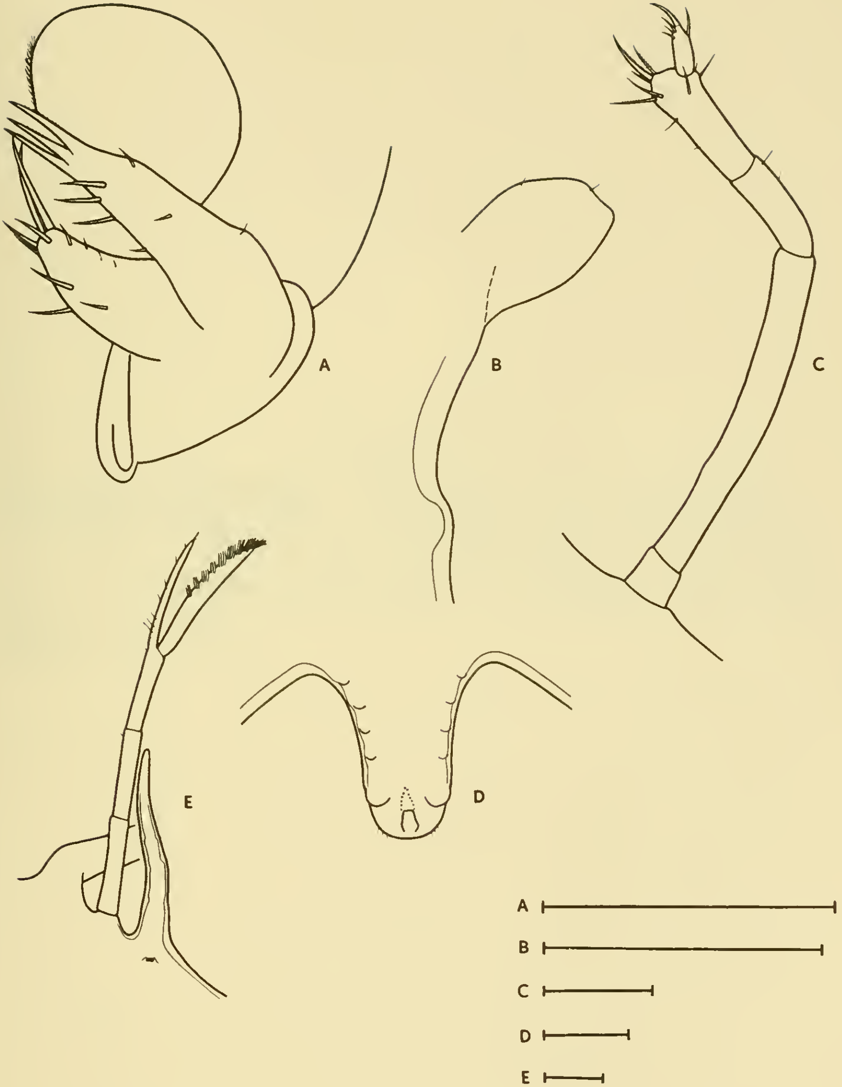

A
B
C
E
D
A
B
C
D
E

Figure 98

Parribacus antarcticus. Appendages of 65-mm phyllosoma. A, maxilla 1. B, maxilla 2 and maxilliped 1. C, maxilliped 2. D, antennule and antenna. E, abdomen. All scales represent 1.0 mm.

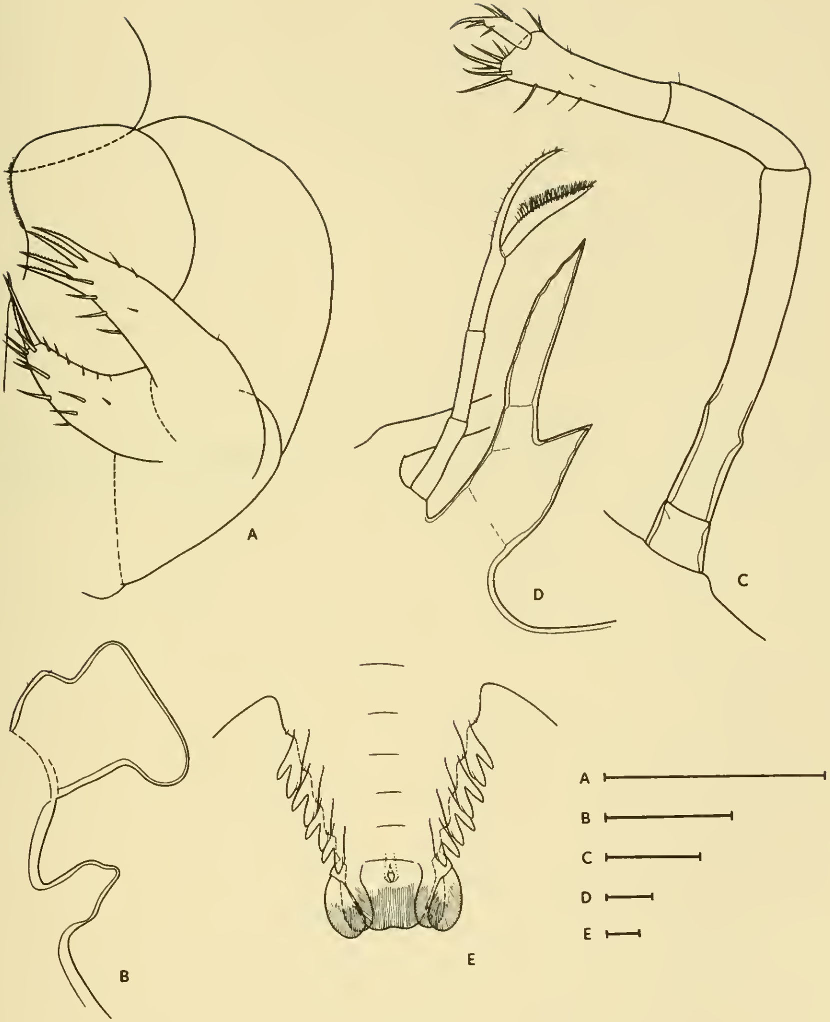
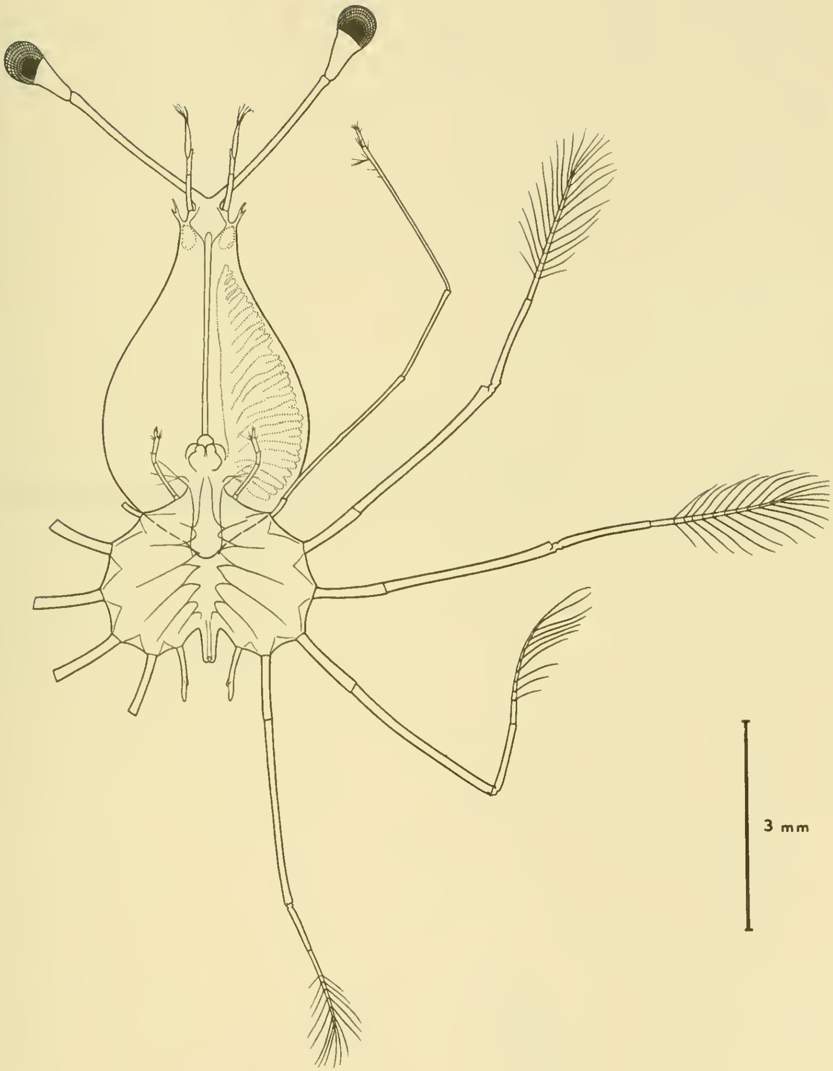

A
D
C
B
E
A
B
C
D
E

Figure 99

?Arctides guineensis. 6.6 mm, plankton.



3 mm

Figure 100

?Arctides guineensis. 8.6 mm, plankton.

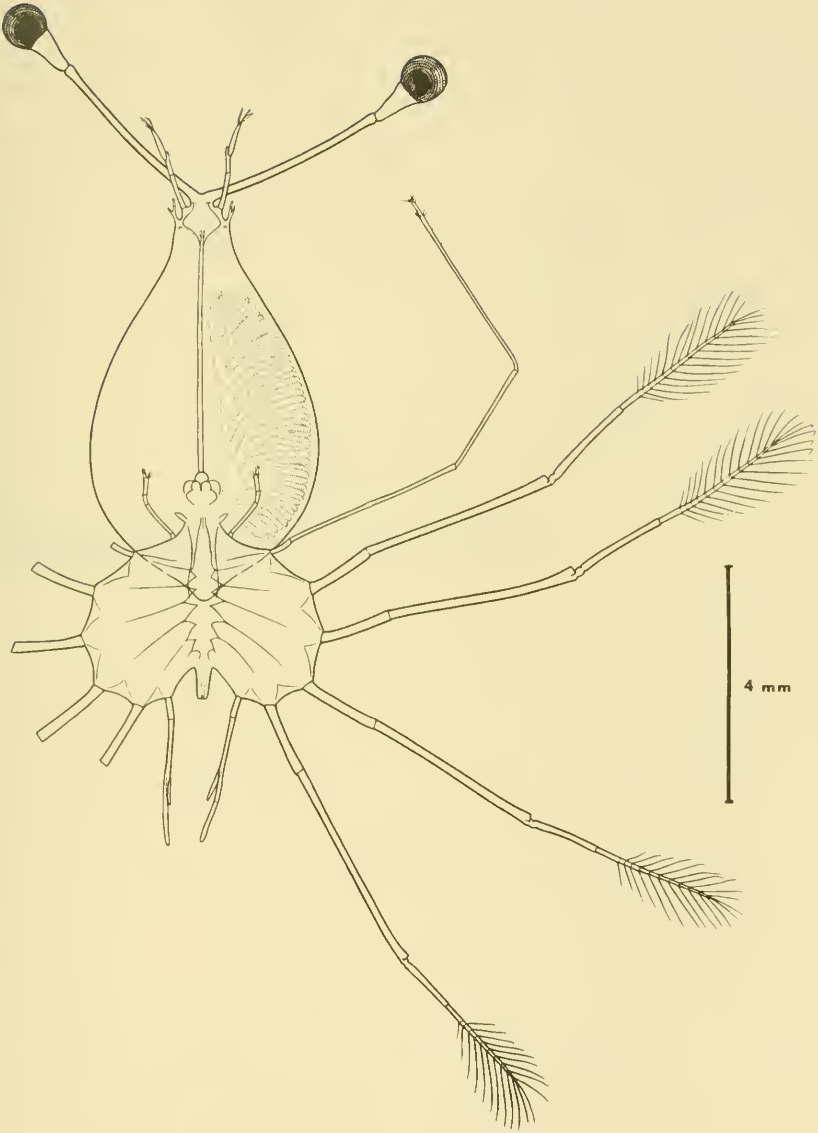

4 mm

Figure 101

?Arctides guineensis. 11.6 mm, plankton.

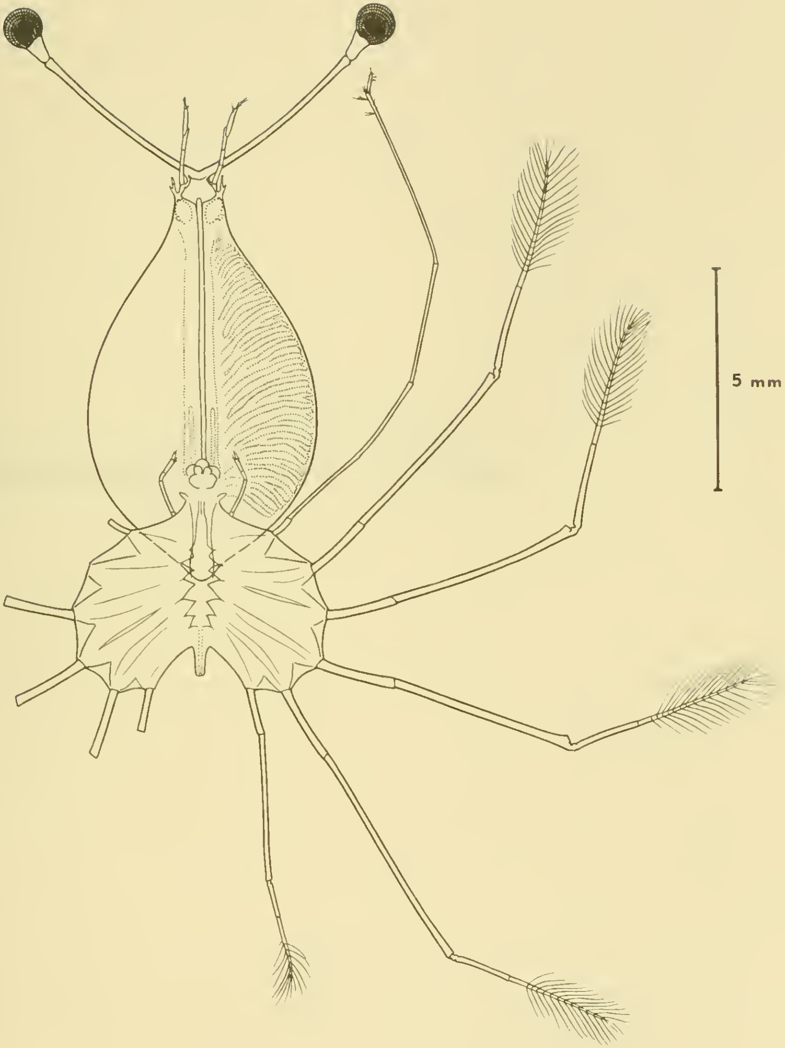

5 mm

Figure 102

?*Arctides guineensis*. 16.6 mm, plankton.

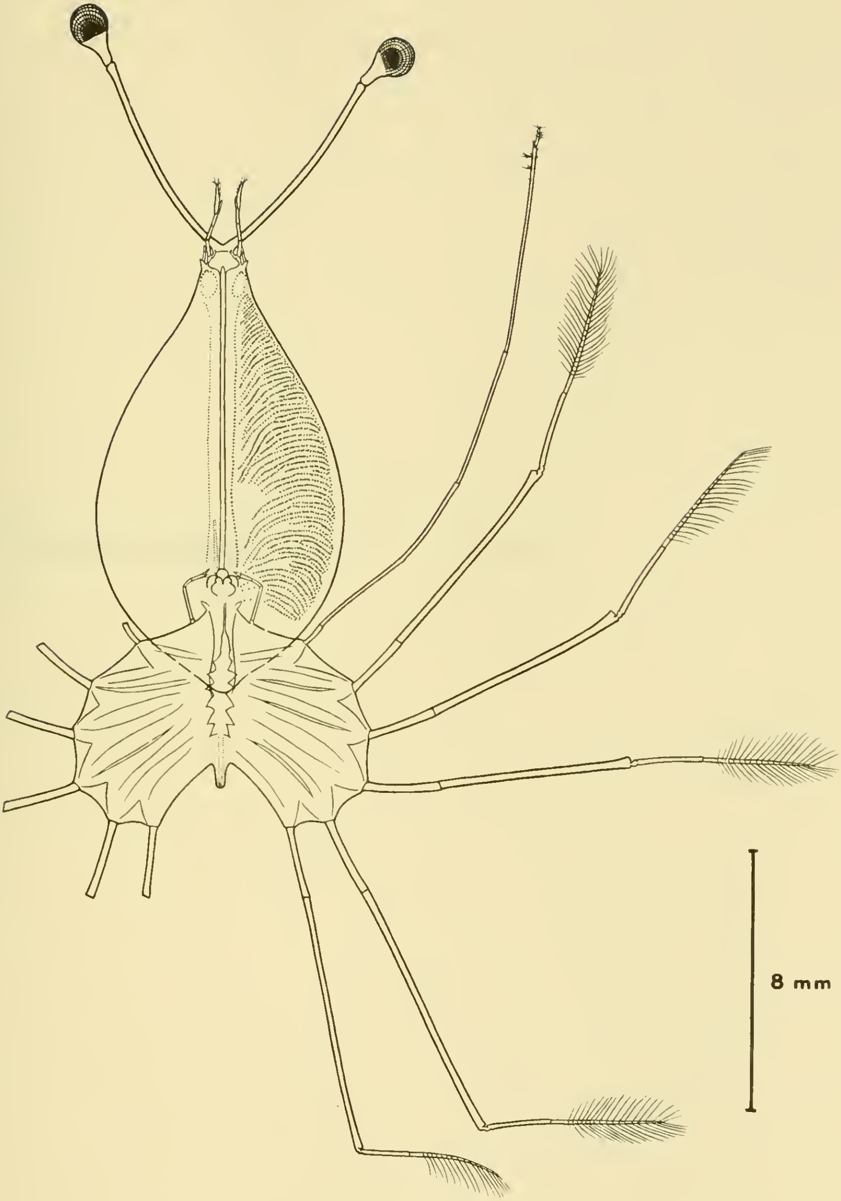

8 mm

Figure 103

?*Arctides guineensis*. 29.0 mm, plankton.

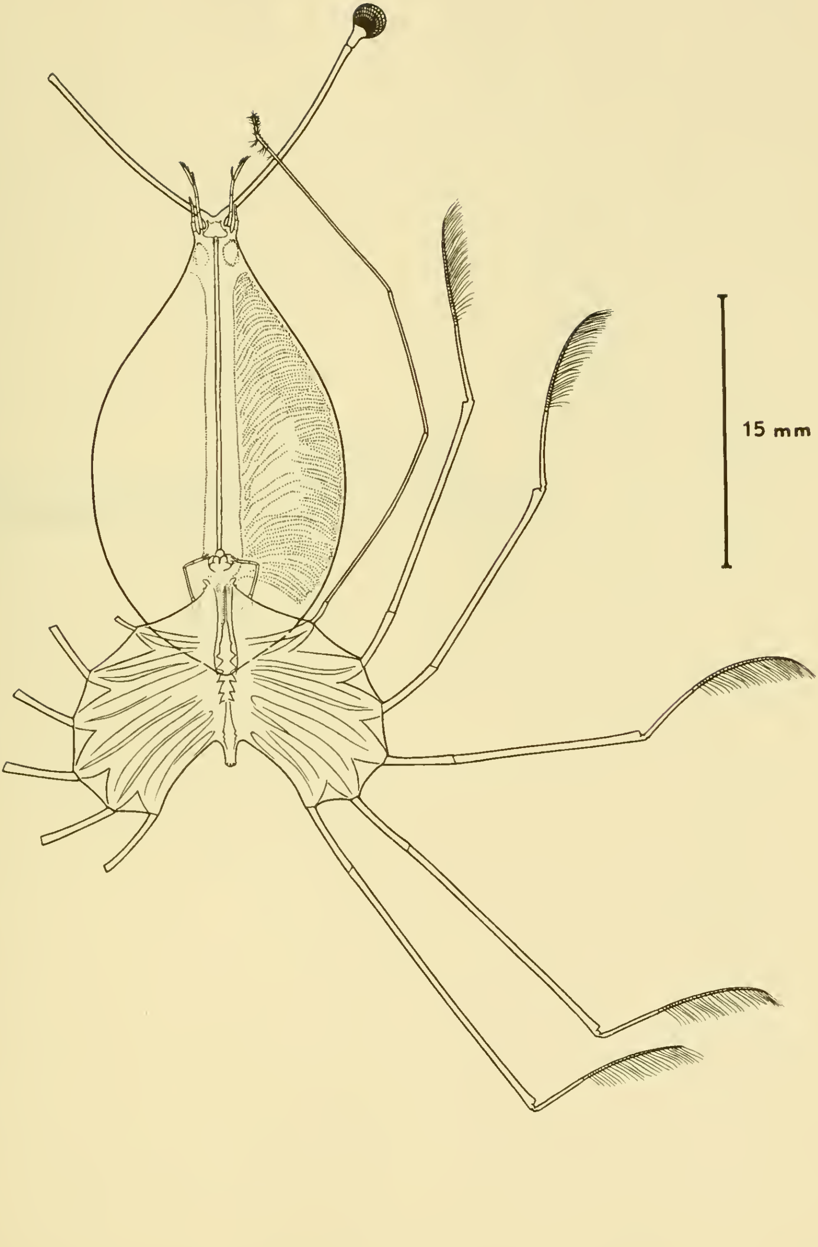

15 mm

Figure 104

?Arctides guineensis. 49.5 mm, plankton.

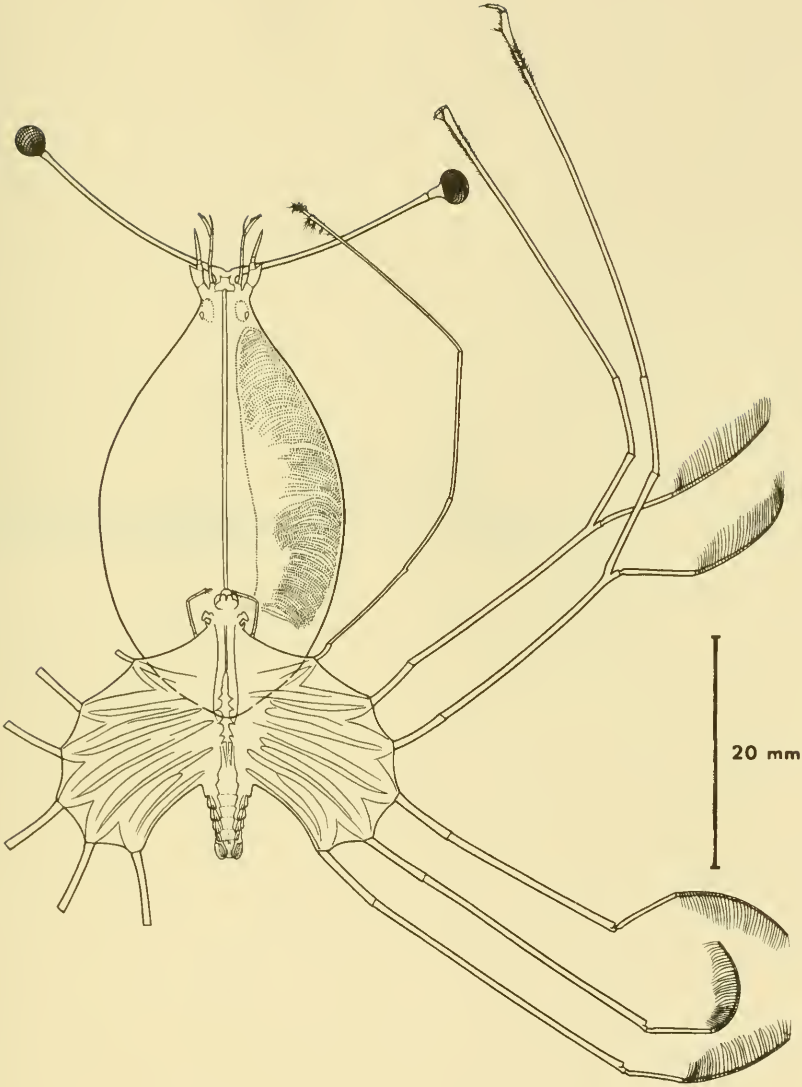

20 mm

Figure 105

?*Arctides guineensis*. 59.2 mm, plankton.

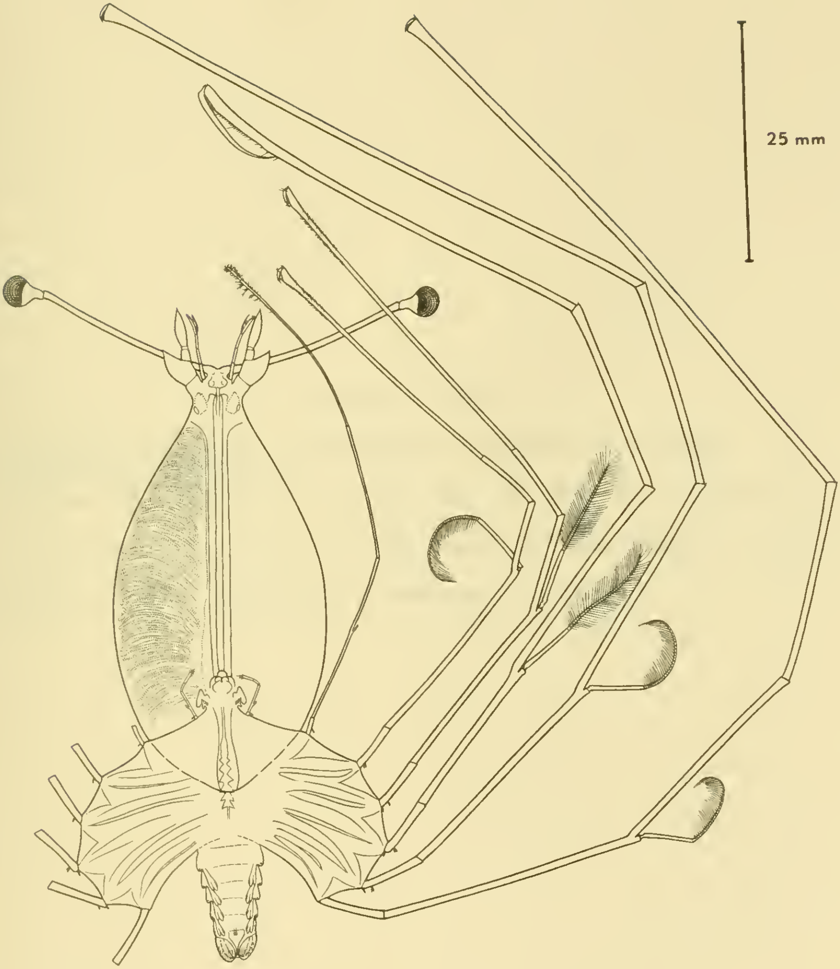

25 mm

Figure 106

?Arctides guineensis. Abdomen of phyllosoma stages. A, 6.6 mm. B, 11.6 mm. C, 16.6 mm. D, 29.0 mm. E, 49.5 mm. F, 59.2 mm. Scales AC, B represent 0.5 mm; scale D represents 1.0 mm; scales E, F represent 3.0 mm.

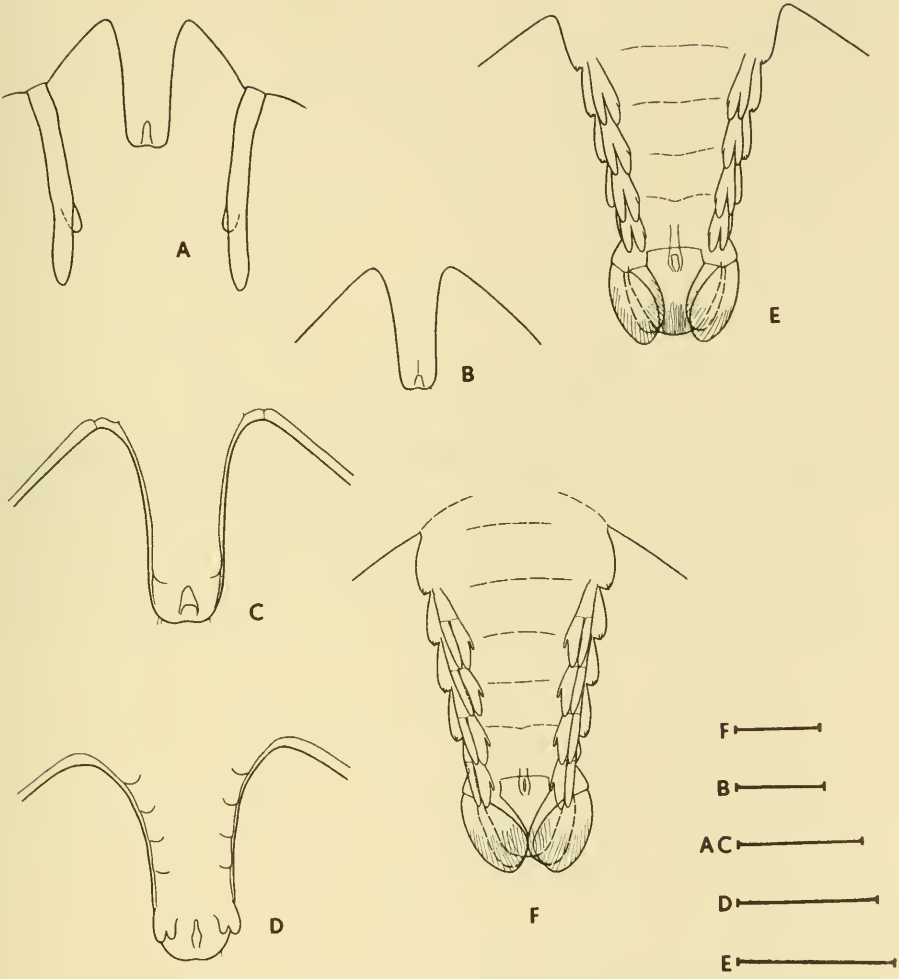

A
B
E
C
D
F
F
B
A C
D
E

Figure 107

?*Arctides guineensis*. Antennule and antenna of phyllosoma stages. A, 6.6 mm. B, 8.6 mm. C, 11.6 mm. D, 16.6 mm. E, 25.0 mm. F, 29.0 mm. G, 49.5 mm. H, 59.2 mm. Scales AB, CD represent 0.5 mm; scales EF, G, H represent 1.0 mm.

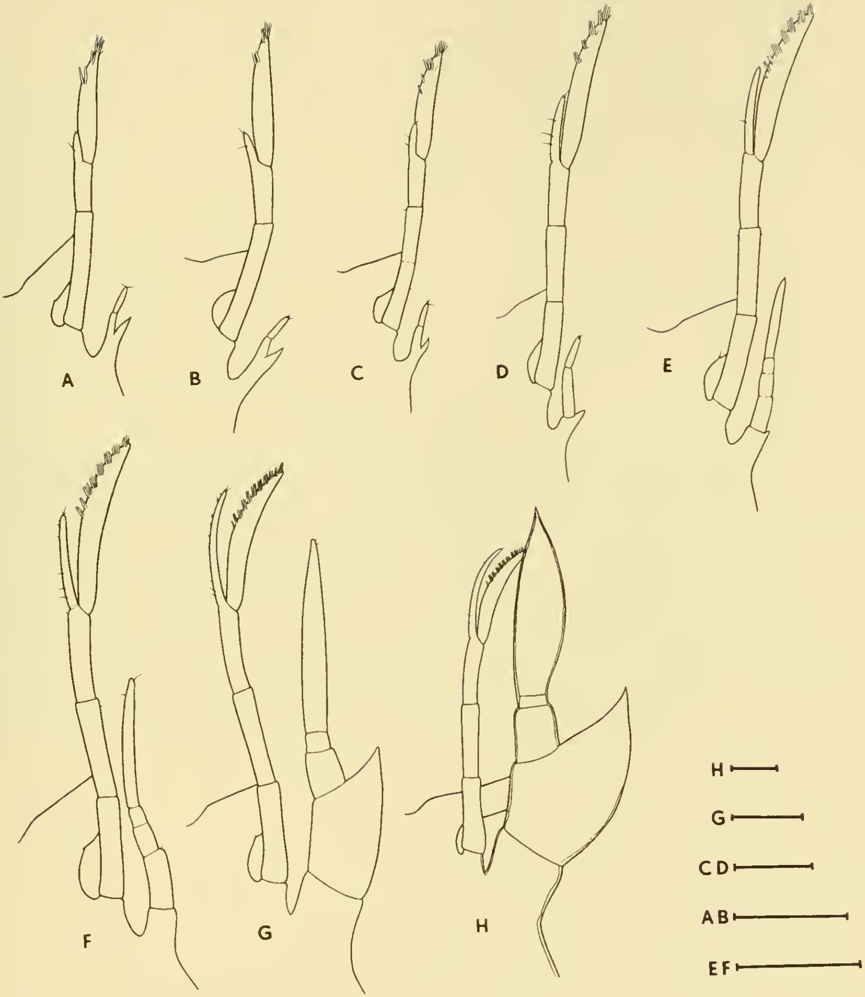

A
B
C
D
E
F
G
H
H
G
C D
A B
E F

Figure 108

?Arctides guineensis. Mouthparts of phyllosoma stages. A, maxilla 2, 6.6 mm. B, same, 8.6 mm. C, same, 11.6 mm. D, maxilla 2 and maxilliped 1, 16.6 mm. E, same, 29.0 mm. F, same 49.5 mm. G, same, 59.2 mm. H, maxilla 1, 6.6 mm. I, same, 59.2 mm. Scales ABCDH, E represent 0.2 mm; scale I represents 0.5 mm; scale FG represents 1.0 mm.

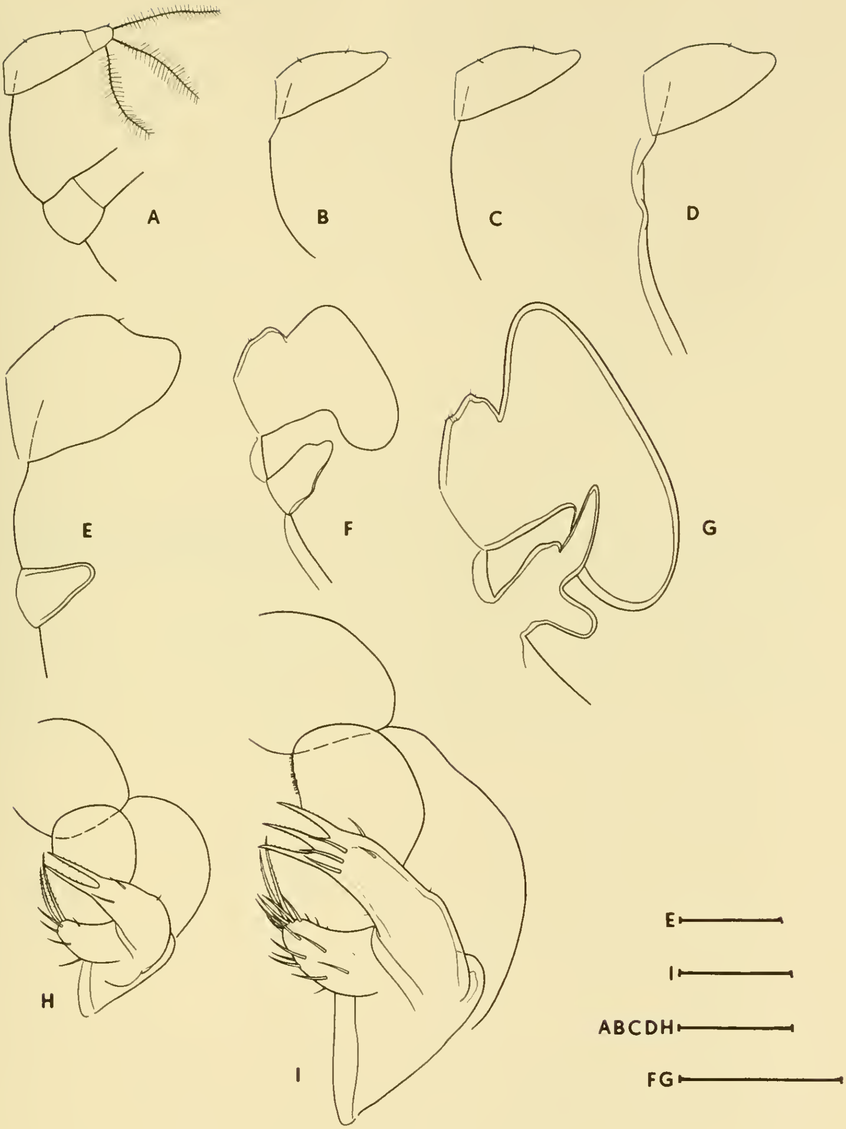

A
B
C
D
E
F
G
H
I
E
I
ABCDH
FG

Figure 109

?Arctides guineensis. Appendages of phyllosoma stages. A, B, C, D, E: distal end of pereiopods 1-5 respectively, 59.2 mm. F, maxilliped 2, 8.6 mm. G, same, 49.5 mm. H, same, 59.2 mm. Scale A-E represents 3.0 mm; scale GH represents 1.0 mm; scale F represents 0.5 mm.

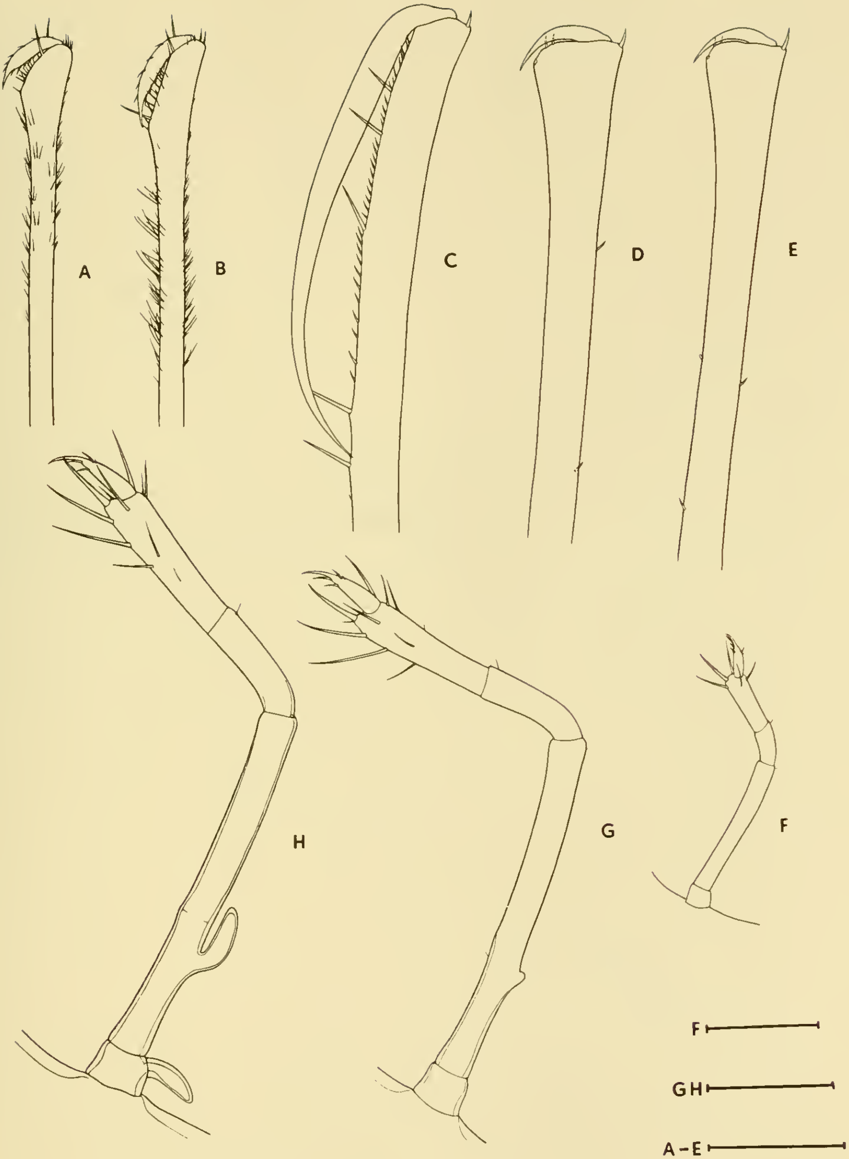

A
B
C
D
E
H
G
F
F
GH
A – E

Figure 110

Phyllosoma Q. 10.8 mm, plankton.

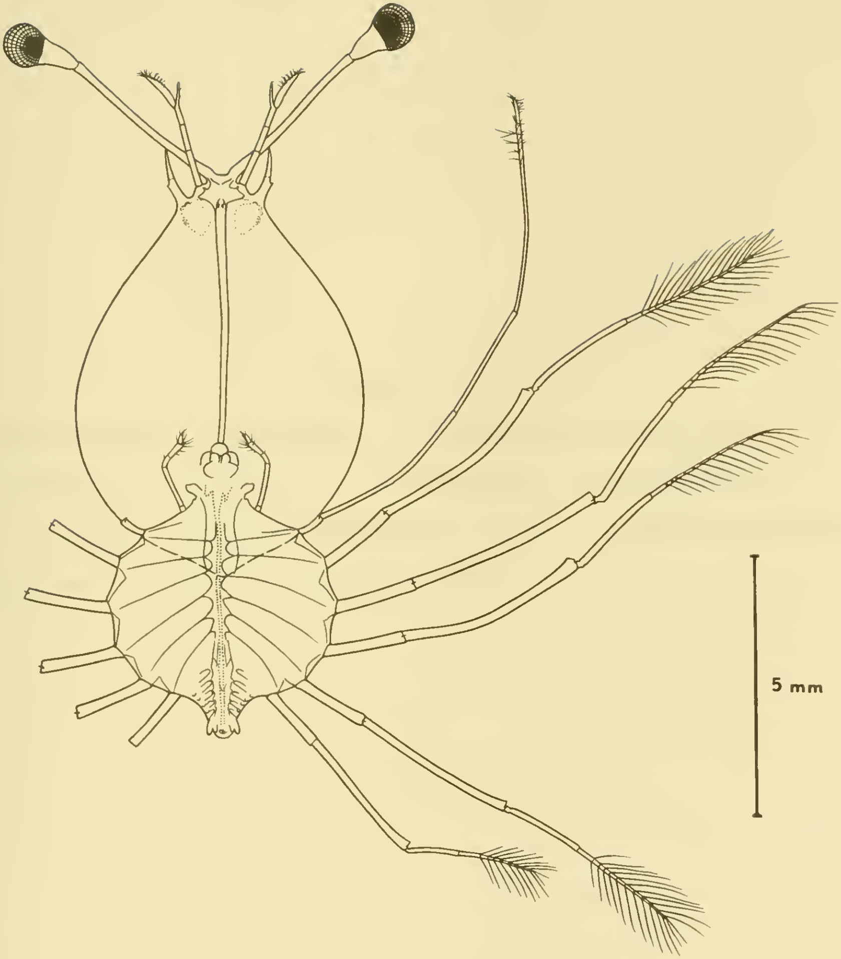
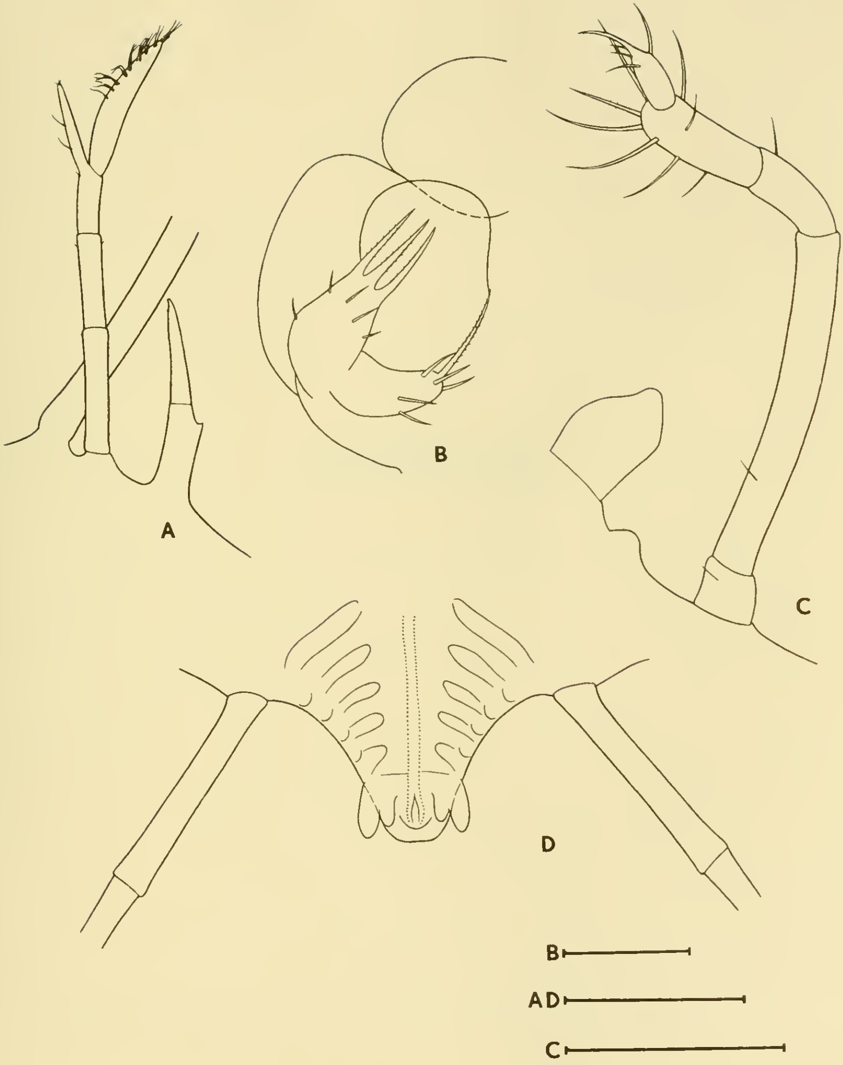

5 mm

Figure 111

Phyllosoma Q. Appendages. A, antennule and antenna. B, maxilla 1. C, maxilla 2, maxilliped 1 and maxilliped 2. D, abdomen. Scale AD represents 1.0 mm; scale B represents 0.2 mm; scale C represents 0.5 mm.


A
B
C
D
B
AD
C

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VITA

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